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ECOLOGICAL OBSERVATIONS ON THE FISHES OF KASHMIR AND INDIAN TIBET

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INTRODUCTION

The present paper is based on observations made in Kashmir and in Indian Tibet (Ladak and Rupshu) during the course of the Yale North India Expedition in 1932. Practically all the individual records of the species of fishes collected have already been published by Dr. Sunder Lal Hora (1936) and by the late Mr. Dev Dev Mukerji (1936), but it is believed that sufficient new and interesting data, relating to zonation of streams and to the distribution of limnetic species of Nemachilus, have been assembled to justify publishing all the relevant information in a separate contribution.

Without the invaluable taxonomic studies of Dr. Hora and Mr. Mukerji, the present paper could not have been written; it gives me particularly pleasure to express my gratitude to Dr. Hora, in view of the fact that a lecture given by him some years ago first aroused my interest in the problems here discussed. To Dr. Hellmut de Terra, leader of the Yale North India Expedition, I am indebted not merely for help and encouragement in the field, but also for continued opportunity to discuss the geological problems involved. My best thanks are also due to the late Professor Silvain Levi and to M. E. Benveniste for information relating to an inscribed rock at Tangtse, and to Professor Alexander Petrunkevitch for assistance with Russian literature.

THE SPECIES OF THE KASHMIR VALLEY

The Kashmir valley is a well-watered fertile plain (Fig. 1), lying for the most part at an elevation of about 1580 m., between the Pirpanjal Mountains and the main range of the Himalaya. During the great part of the Pleistocene, a very large fresh-water lake occupied the basin; the deposits of this, the Karewa Lake, constitute the existing surface of the valley plain. Across this plain the River Jhelum flows; it is a relatively mature stream, forming beautiful meanders. Numerous lakes and swamps occur along its course and in the courses of its tributaries. None of these lakes is deep. The deepest, Lake Manasbal, has a maximum depth of 12.8 m. The other three principal lakes, Wular, Bod Dal and Lokut Dal are much shallower and are almost entirely carpeted with flowering plants. In the vicinity of Srinagar, large swamps exist on the western side of Lokut Dal; these swamps are extensively canalised and are cultivated by the mooring of rafts, called floating gardens, laden with mud and manure, on which tomatoes and other vegetables can be grown. Very large amounts of nutrient substances must therefore pass into the waters of the lakes and swamps. Plankton was

not richly developed in the lake water at the time of my investigation, but the productivity of these waters in rooted vegetation must be enormous, providing food and cover for immense numbers of fishes. Very large quantities of fish are caught annually, chiefly by cast-nets and by spearing. The human activities of the region center so clearly around the aquatic biocoenosis, that any further artificial control of the environment that might be considered in the future would have to be undertaken with the greatest possible care, in order to avoid disturbance of the biological cycles in the water.

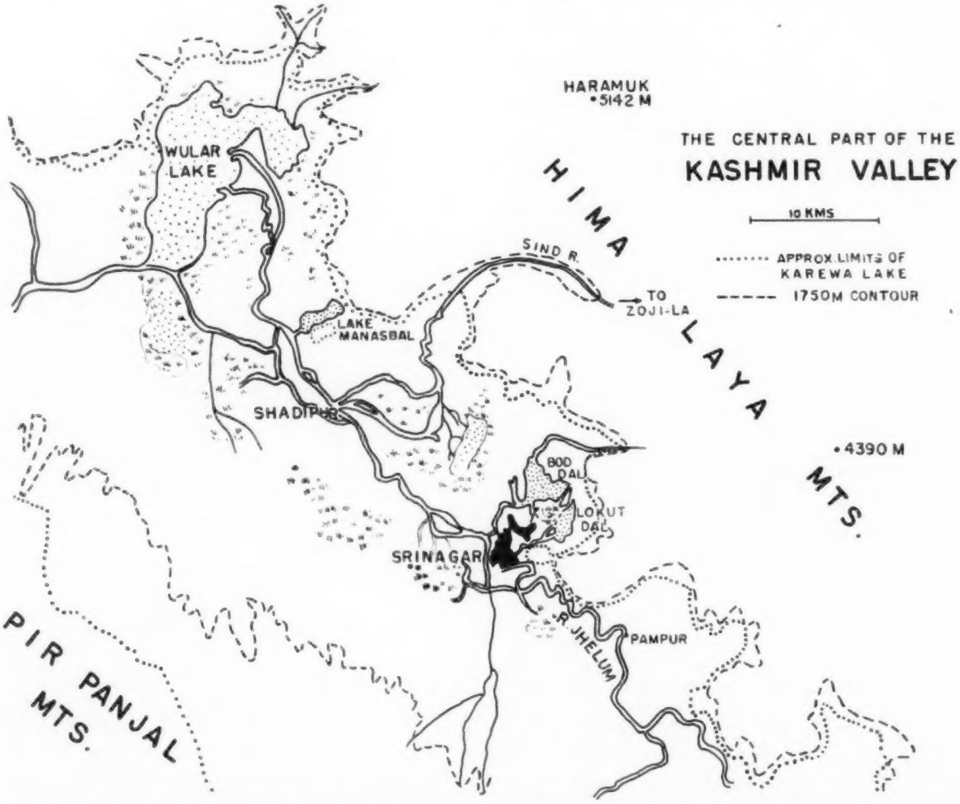

FIG. 1. The central part of the Kashmir Valley, showing the positions of localities mentioned in the text. The approximate shore-line of the Karewa Lake, raised by post-Karewa earth-movements on the southwest side of the valley, is based on the results of Dainelli (1922).

TEMPERATURES AND CHEMICAL OBSERVATIONS

During April, observations of surface temperature ranging from 15.85°C (Bod Dal, 6.45 A.M. April 6, 1932) to 19.85°C (midday, Manasbal Lake, April 21, 1932) were made. Much higher temperatures must occur in summer. The streams, such as the Sind River, which flow directly from the Himalayan snows are doubtless always cooler than the other waters; no fishes were obtained in such rivers, but the mahseer (*Barbus tor* Ham - Buch) a well-known game fish, is said to enter these colder waters in prefer-

ence to ascending the warmer Jhelum. Otherwise temperatures probably play little or no part in regulating the local distribution of fishes in the waters of the flat central part of the valley.

The oxygen contents of the surface waters of the lakes varied from 7.4 to 10.9 mgrms. per litre; lower values doubtless occur in the summer, but it is again improbable that differences in oxygen content are of any great importance in regulating the local distribution of fishes. The same is also true of alkalinity (bicarbonate) which varied between 0.0014 N. and 0.0019 N. and of pH (8.2 to 9.0).

It is, however, not impossible that the Himalayan streams flowing down the humid and well-forested southwestern slopes of the main range support a truly stenoxybiont, cold stenotherm fauna. Observations made in the Sind River at Gund at an altitude of only 2080 m. on May 17, gave a temperature of 8.6°C and an oxygen content of 9.2 mgrms. per litre. In this region even at the height of summer, it is unlikely that the water ever reaches the temperatures found (up to 23°C) in the afternoon in the semi-desert country at greater altitudes within the range, nor would the oxygen contents be as low as those of streams at greater altitudes. Further investigation may indicate that certain fishes, such as *Nemachilus kashmirensis* Hora, not obtained by the expedition but recorded from springs and streams within the region, are characteristic of such cool and well-oxygenated water. The same may be true of other animals such as *Euplanaria* sp. found at Gund, and at no other place where collections were made (Hyman 1934), and of some of the endemic water-mites described from the Himalayan slopes and colder springs of the country immediately to the northeast (Lundblad 1934).

VEGETATION AND RATE OF FLOW

The lakes and swamps of the valley are, except for Wular Lake, practically free from suspended mud, and are all richly carpeted with rooted aquatic plants down to about 4 m. The canals and rivers are normally slow or moderate flowing and easily navigated by small boats paddled by hand. At times of flood, the flow is doubtless very rapid, at other times the flow in the canals is regulated by means of sluices. All the river water is turbid with mud, rooted vegetation is scarce or absent, and much deposition is occurring where the Jhelum enters the Wular Lake.

This contrast in the nature of the two types of habitat is of paramount importance in determining the local distribution of fishes, though it is not clear whether the rate of flow or the nature of the bottom is of greater importance. The observations bearing on this matter may be summarized as follows.

COBITIDAE

Nemachilus vittatus (Heckel) is apparently strictly limnobiont. It was not, however, obtained in the Dal Lakes, though it is abundant in the Wular

Lake and in a pond at Shadipur. Most of my material was secured from fishermen who use this species as bait. It is probably to be regarded as a littoral fish.

Botia birdi Chaudhuri was only obtained from the Jhelum. The observations are inadequate to permit an opinion on its status.

Cyprinidae-Schizothoracinae

Schizothorax esocinus Day, was once brought me from Lokut Dal, where it is definitely very much rarer than the next two species. One was caught in a canal and four from the Jhelum itself. The species is undoubtedly to be regarded as rheophil.

S. micropogon Heckel and *S. planifrons* Heckel, particularly the latter, are the commonest fishes of the lakes, though both may occur in canals and probably in the Jhelum itself. They may be regarded as limnadophil species, but not very markedly so. Unfortunately these species were wrongly classified in the field so that it is not possible to indicate if they have any habitat differences. Both are apparently equally at home in the lower Dal Lake.

S. longipennis Heckel and *S. curvifrons* Heckel were obtained but sparingly. The former species ascends the Indus as far as Baltistan (Vinciguerra 1930) and is probably rheophil.

Oreinus sinuatus (Heckel) and hybrid forms were obtained only in running water and may be regarded as rheobiont. I have looked over catches made by fishermen on the lakes and have never found Oreinus to be present; the preference of these fishes for moving water is well known to the Kashmiris.

Cyprinidae-Cyprininae

Crossochilus punjabensis Mukerji probably has a similar range of habitats as *Schizothorax planifrons.* Not enough information was obtained about *Labeo diplostomus* (Heckel), the only other member of the Cyprininae obtained.

Sisoridae

Glyptothorax kashmirensis Hora was brought to me from the Jhelum and I was shown very sluggish muddy canals where the fish was said to occur, though none were obtained. The species is probably found primarily in running water, but it is in no sense a torrential fish. It is very doubtful whether an adhesive apparatus on its ventral side would ever be required to maintain a position against the gentle current in the habitats of the species, though it is possible that it is of assistance in feeding, as Hora ingeniously suggests. The whole structure is however so soft, particularly in life, that I cannot help suspecting that in *G. kashmirensis* it is largely vestigial, a view with which Hora would appear in part to concur.

FEEDING HABITS

The food preferences of the commoner Schizothoracinae were studied by examination of the gastro-intestinal contents of the specimens obtained. Unfortunately the material referred to *Schizothorax planifrons* and *S. micropogon,* was, in the field and in the preliminary laboratory determinations, wrongly separated as *S. planifrons* ("Chush") and *S. niger* ("Alghard"), the latter species being probably a synonym of the former. Some of the individual tags having become obliterated in the transport of the specimens, it is now not certain to what extent *S. micropogon* is represented in the series of specimens examined, though probably the specimens recorded as *S. niger* were really of the species. The two groups show identical feeding habits.

S. planifrons and *S. micropogon.* Of the sixteen specimens examined, four were empty, three contained certain molluscan remains and four animal matter, probably molluscan; the remainder contained filamentous algae, remains of flowering plants, and in one case, of a beetle. None contained any vertebrate remains, and no sand or mud was noted.

S. esocinus. Of six specimens examined, four were entirely empty, one contained animal remains probably musculature from a much digested piece of a fish; one, from Lokut Dal Lake, contained indeterminate animal matter and two very small pieces of pond weed. This species is said by Hora to be carnivorous; such is also the opinion of the Kashmiris who maintained that it is always obtainable with live bait, which only will attract the very largest specimens of "chush" *(S. planifrons).*

Oreinus sinuatus. One specimen from a canal at Srinagar contained a little brown detritus and two algal fragments in the intestine. The stomach was empty and the fish had clearly not been recently feeding. Of six specimens from the Jhelum, one was empty, the other five contained greater or lesser amounts of mud and sand, in one case with remains of an oligochaet, in another with indeterminate animal matter. Three hybrids, Oreinus x Schizothorax from the Jhelum were also opened. One was empty, of the other two, the specimen nearer Oreinus contained very sandy mud, the specimen nearer Schizothorax remains of seeds (lentils?) thrown into water. The typical specimens of Oreinus clearly feed by taking up large amounts of bottom material indiscriminately. The observation on the hybrids are inconclusive but open up an interesting possibility.[2] It is clear that among the commoner Schizothoracinae of Kashmir, the most limnadophilic species are omnivorous but selective feeders, subsisting on both invertebrates and on vegetable matter, while the most rheobiont species, *Oreinus sinuatus,* feeds indiscriminately on the vegetationless bottom of its habitat; *Schizothorax esocinus,* intermediate between these two in its habitat preference,

[2] If Berg is correct in his belief that *S. curystomus* Kessler is but a variety of *S. intermedius* (McClelland) and that species both with and without a well-developed horny lip belong in Schizopygopsis and in Dyptichus, it is clear that the less selective method of feeding has arisen several times from the more selective, and that structures appropriate to either method may occur within a species. A further analysis of hybridisation might give results of great evolutionary significance.

appears to differ from both in its food, though the latter, probably consisting largely of small fishes, could be equally well obtained in either running or still water. These observations suggest that the nature of the bottom and the food that it supplies may be as important in determining the distribution of these forms in the Kashmir Valley as is the primary distinction between still and flowing water.

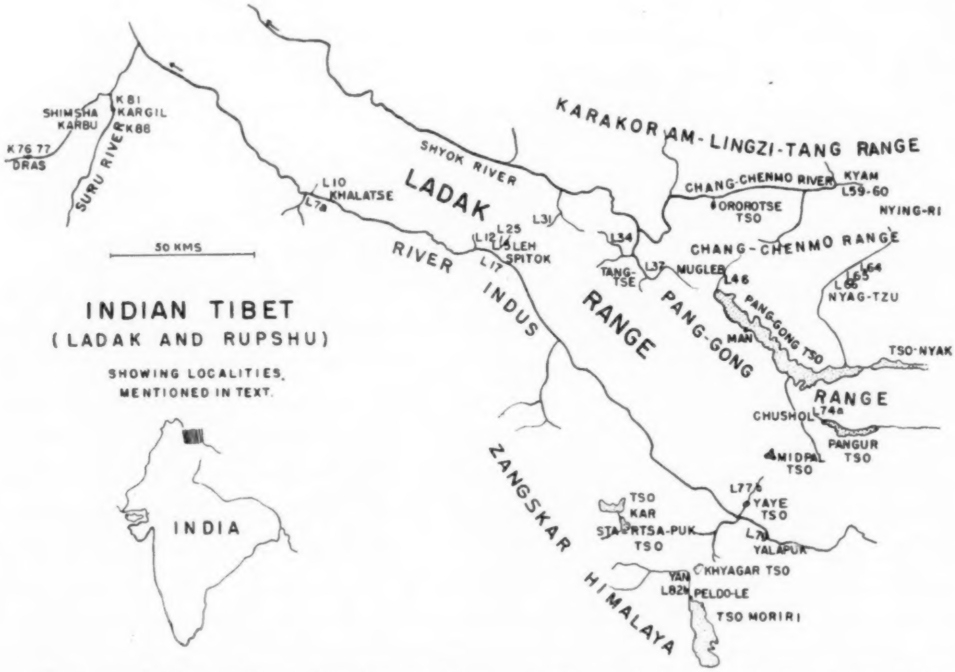

Fig. 2. Indian Tibet, showing positions of the collecting stations of the Yale North India Expedition, mentioned in the text.

Parasitism

Datta (1936) records two species of Eosentis, *E. devdevi* from *S. planifrons* and *E. yalei* from *S. esocinus,* as parasites of the material collected by the expedition. The only other member of the genus, *E. rigidus* Van Cleave is a parasite of *Schizothorax zarudnyi* Nikolsky in Seistan. While these parasites were not observed in sufficient numbers to suggest that they play a great part in the ecology of their hosts, their occurrence is interesting in that they suggest that the genus Eosentis is restricted to Schizothorax, whereas host specificity in general would appear to be rare in Acanthocephala.

RHEOPHIL AND RHEOBIONT FISHES OF INDIAN TIBET

Proceeding by the usual road from Kashmir into Ladak, once the Zoji-la is crossed, the nature of the landscape changes entirely. Trees are practically absent, being confined to Salix, Populus, Juniperus, and a few cultivated fruit trees in the more sheltered valleys. The vegetation, except in such

sheltered and irrigated valleys and at great altitudes near the snow-line, is xerophytic; small areas of absolute desert are not rare. The high mountains are, however, well glaciated and fresh-water streams are common. In this region most of the fishes were obtained from running water, though some were collected from the numerous lakes that lie to the east of Leh, towards the boundary of Tibet proper. It has been found advisable to discuss the biology of the three species of Nemachilus, confined to the closed lake basins and their immediate vicinity, in a separate section, and the present paragraphs are limited to a discussion of the Schizothoracinae, Sisoridae and rheophil species of Nemachilus.

CLASSIFICATION OF LOTIC HABITATS

Since most of my time was spent in the investigation of the lakes of Indian Tibet, physico-chemical observations on the streams are not as complete as might be desired. In particular, it was not possible to make accurate determinations of the rate of flow, but in a number of cases, very rough and probably minimum judgment of the rate of descent of floating objects has permitted a classification of streams into rapid (5-20 m. per minute) and torrential (over 20 and often over 60 m. per minute). Streams are further classified as small when they are under two meters wide, and if wider are very shallow, and large when they are from two to five meters wide, and have holes up to one meter deep. Larger habitats are regarded as rivers. The two investigated, the Suru at Kargil, and the Indus at Khalatze, Spithug and Yalapuk, differ from the large streams in being very turbid. The turbidity is primarily due to inorganic material.

Since practically all the fishes collected have been enumerated by Hora (1936) and by Mukerji (1936), no complete list of records is necessary here. The various stations, the positions of which are indicated on the map (Fig. 2), are, however, roughly classified, using the criteria already discussed.

I. Small streams (all may be regarded as rapid)
   K76, K77, K83, L6, L15, L59, L65-66, L74a, L77b, L82b.

II. Large streams
   A. Torrential L12, L31, L34.
   B. Rapid L25, L37, L46.

III. Rivers
   Suru, K88 (rapid to torrential); Indus, L7a, L17, L79 (rapid).

TEMPERATURE AND CHEMICAL CONDITIONS

The temperatures recorded in the streams and rivers of Indian Tibet cover a wide range, from freezing to 24.3°C. Unfortunately, it was not possible to make any regular observations on the diurnal variation of temperatures, but such variation, owing to the rarity of the atmosphere, is

undoubtedly very great, probably usually of the order of ten and possibly of the order of twenty degrees. The highest temperatures recorded for the habitats of the principal species observed are as follows:

Nemachilus gracilis (Day)........24.3°C (Dras K77)
N. stoliczkae (Steind.)........22°C (Tangtse-Mugleb, L37)
Schizothorax esocinus and *S. labiatus* (McClelland)........19°C (marginal temp. of Indus at Spithug)
Orcinus sinuatus........19°C (marginal temp. of Indus at Spithug)
Ptychobarbus conirostris (Steind.)........19°C (marginal temp. of Indus at Spithug)
Dyptichus maculatus (Steind.)........22°C (Tangtse-Mugleb, L37)
Schizopygopsis stoliczkai (Steind.)........22°C (Tangtse-Mugleb, L37)

The stream at Dras, studied on May 21, 1932, would undoubtedly have been warmer at the height of the summer, it is therefore probable that *N. gracilis* is exposed to somewhat higher temperatures than those recorded, which, in the case of the other records, must closely approximate to the highest temperature experienced by the species in question. All of the high altitude fish therefore appear relatively tolerant of high and very fluctuating temperatures; they are, to employ Parr's (1933) useful term, hetero-eurythermal. *N. gracilis* is however, probably more eurythermal than the other species, a fact which may be of zoogeographical significance. All the Schizothoracinae for which any data exist appear to be summer breeders (Stewart 1911, Berg 1932). Stewart's observations are confirmed by the presence of ripe females among the specimens of *Schizothorax stoliczkae* collected in the Tangtse-Mugleb stream. Hora's observations on the state of the ovaries in my specimens of Nemachilus also suggest that these fishes breed at the warmest time of year. Tolerance of temperatures of over 20°C is therefore apparently shown by the eggs and young as well as the adults of the species studied.

The oxygen content was investigated only in the streams at Dras and at Chagra (L46). In the former at 5.15 p.m., when the temperature had fallen from 21° and 24.5° in two different parts of the stream examined at 3 p.m. to 16° and 19°, the oxygen content was 6.7 and 6.2 mgrms. per litre respectively. At Chagra at a temperature of 14.2° the oxygen content was 6.4 mgrms. per litre. It may be noted that at the altitude of Kyam, the highest station for *N. gracilis*, where the water had a temperature of 13.2°C. the value of saturation would be 5.32 mgrms. per litre, while at the altitude of the Tangtse-Mugleb stream at 22°C it would be 5.25 mgrms. per litre. The water of all the streams of the region is practically colorless, and must be very low in organic content so that a deficit is not to be expected: the surface waters of the lakes are usually supersaturated. The entire range of observations (cf. Hutchinson 1937) lies between 5.4 and 7.7 mgrms. per litre. The limiting oxygen contents of the habitats of the rheophil fishes may therefore safely be set as 5 and 8 mgrms. per litre, lower temperatures

roughly compensating for decrease in atmospheric pressure with increase in altitude. Though this range is below that to be expected in the low-lying but cool streams of the southwestern Himalayan slopes of Kashmir, as typified by the Sind River at Gund, it is most unlikely that oxygen deficiency plays any part in the ecology of the high altitude fish fauna. In North America, a stream can support a fair population of brook trout, *Salvelinus fontinalis* (Mitchill), when its oxygen tension is reduced to 2.4-3.7 mgrms. per litre (Creaser 1930); other groups of fishes, less stenoxybiont than the Salmonidae, require a minimum of less than two milligrams per litre. Since at the low temperatures prevalent at high altitudes, in the absence of appreciable amounts of reducing substances, the atmospheric pressure would have to be reduced to about one quarter of its value at sea-level, below that corresponding to the summit of Mt. Everest, to produce such oxygen tensions, it is clear that oxygen deficiency produced by altitude alone can play no part in limiting the vertical distribution of fishes.[3]

The streams and rivers of Indian Tibet appear to contain slightly alkaline water, the range in values of the alkali reserve (0.0007N. in K77 at Dras to 0.0023N. in the Indus at Spithug) being similar to that observed in the open lakes (Hutchinson, 1937). The pH range in the streams and rivers is from 7.8 to 8.5. Somewhat higher values may occur in the weedy open lakes, Sta-rtsa-puk Tso reaching over 9.6. The values for the alkali reserve in all the fresh-water localities are low compared with those of some of the closed habitats of limnetic species of Nemachilus. The relatively small range of variation in the fresh-water localities and in particular the absence of acid water in the region, indicates that chemical factors play little part in the ecology of the stream and river fishes of the region.

THE SPECIES OF THE SMALL STREAMS

The Rheophil species of Nemachilus. Rheophil species of Nemachilus occurred in all the small streams except L6, in which only *Glyptosternum reticulatum* McClelland was obtained. This stream, however, differed in no apparent way from other members of its group and it is probable that if more time had been available for its investigation, specimens of Nemachilus would have been obtained (Fig. 3).

Dyptichus maculatus was obtained in one of the localities regarded as a small stream (L15), that flows between the Bazaar and the Residency at Leh. This is used for washing clothes, but the fauna appears to be unaffected by such activities. In the upper reach investigated, the stream contained a number of holes and in these Dyptichus was common; lower down it became wider but very shallow, and there only *Nemachilus stoliczkae* was obtained. The upper part of the stream is to be regarded, on account of its

[3] Some rather crude experiments indicate that in both *Schizothorax* sp. (*micropogon* or *planifrons*) and in *Dyptichus maculatus*, about 10 per cent of the total oxygen uptake is dermal. The reduction of scales in Dyptichus and Schizopygopsis therefore appears to have no respiratory significance, a conclusion in agreement with Annandale and Hora (1920).

greater local depth, as a transition to the next category. A second record of a very young specimen of *D. maculatus,* from a spring at Chagra, is to be explained by the fact that numerous adults of the species occurred in the large stream at that place and that the streamlet from the spring joined the large stream a few meters below its origin.

A few young *Schizopygopsis stoliczkae* were similarly noted in the very short stream that entered the western end of Pangur Tso, and in a very shallow branch of the stream below Chagra, which branch rejoined the main stream lower down.

Fig. 3. A typical small rapid stream, L6. Kalatse. Habitat of *Glyptosternum reticulatum.* Comparable streams elsewhere yielded the majority of specimens of *Nemachilus gracilis* and *N. stoliczkae.*

It is clear that in Indian Tibet, Nemachilus is the characteristic fish of the smaller streams, and that apart from the rarer occurrence of Glyptosternum, other types only occur when young specimens have exceptional opportunities of entering the small streams from their more normal habitats.

In the nine small streams yielding Nemachilus, four contained *N. gracilis,* three *N. stoliczkae,* one the limnadophil *N. panguri* Hora, and one *N. microps* (Steind.). *N. panguri* had undoubtedly entered L74 from Pangur Tso; little can be said about *N. microps* from L82b, the Yan, the northern influent of Tso Moriri, save that its habitat was essentially like those in which the other species were taken. The two commoner species, however, raise

certain interesting problems, and though neither is confined to small streams, a discussion of these problems may not be out of place.

Of the nine localities for *N. gracilis*, four are small streams, two are large streams, one is the Indus River at Yalapuk; the only standing waters in which the species was obtained was the shallow lake Sta-rtsak-puk Tso, which is in communication with a small stream, and a spring-fed pool at Kyam (L60). Similarly *N. stoliczkae* was found in seven localities of which four were small streams, one a pool probably cut off earlier in the year from such a stream, one a large stream and one the freshwater lake, Yaye Tso, which lies in the course of a small stream. Both species may be regarded as rheophil; as Hora very reasonably suggests, it is not unlikely that they resort to the quietest water available for breeding. In three of the small streams in which *N. stoliczkae* was found, my notes indicate that the fish lived in holes between the more rapid reaches, but it can undoubtedly negotiate a very swift current between such holes, by making sudden darts. Such habits are doubtless exhibited by all the stream loaches of the region, and it is easy to understand that a functional swim-bladder would be a useless organ under such circumstances.

In general, *N. gracilis* and *N. stoliczkae* do not appear to inhabit the same stream. The only exception to this rule was L37, where the latter species was however much commoner. In the region studied *N. gracilis* appears to have a slightly lower altitudinal range (2679 m.-4725 m.) than *N. stoliczkae* (3506 m.-4901 m.). The overlap would hardly permit any significance to be attached to these figures, were it not for the fact that they are confirmed by the collected records of other investigators. Thus *N. gracilis* is known to occur within eight miles of Attock, in the North West Frontier Province, at an altitude of less than 500 m. In Indian Tibet *N. stoliczkae* is not recorded from below Nima (alt. c. 3100 m. cf. Hora and Mukerji, 1935) and not certainly from below 2900 m. in Turkestan (Hora and Mukerji, 1935); though some of the Russian records may refer to genuine occurrences of this fish at slightly lower altitudes, it certainly is never found at such low elevations as that of the Attock station for *N. gracilis*. As has been pointed out, it is probable that *N. gracilis* is more tolerant of high temperatures than is *N. stoliczkae*; the lower range of the former species would be easily explained by such a difference. The upper range of *N. gracilis* appears to be delimited by my records from Kyam at 4725 m. (L59, L60), but Zugmayer (1910) has taken *N. stoliczkae* in an affluent of Apo-tso, at 5370 m., and in the effluent of a hot spring south of Lake Mangzaka, at c. 5400 m., the most elevated locality from which any fish has yet been recorded. The whole range for *N. gracilis* would therefore appear to be c. 500 m.-4725 m., and for *N. stoliczkae* c. 2900 m.-5400 m. Though it is possible that *N. stoliczkae* can live permanently at lower temperatures than can *N. gracilis*, and so attain to higher altitudes, it is more likely that *N. stol-*

iczkae is able to colonize streams providing less food than is required by *N. gracilis*. Certainly some of the streams inhabited by the former are extraordinarily barren; in long reaches of the stream above Nyag-tzu (L65-66) which provided my highest records for *N. stoliczkae* no organisms of any sort could be discovered. On the other hand in the vicinity of the highest locality for *N. gracilis* a number of mayflies (*Ameletus primitivus* Traver, in press) and caddisflies (*Pseudohalesus aberrans* Mosely and *Apantaniana hutchinsoni* Mosely, 1936) were obtained; some had probably bred in the stream. As far is known, there is no qualitative difference in the feeding habits of the two species; Hora (1936), largely on the basis of my material, finds that both fishes feed on insect larvae and on the slime encrusting rocks and stones.

A curious correlation was observed between the presence of *N. gracilis* and the turbellarian *Polycelis tibetica* Hyman. In the five streams in which only *N. gracilis* was present (K76, K77, K83, L25,[4] L59), *P. tibetica* was also found, while in none of the streams inhabited by *N. stoliczkae* did the turbellarian occur. Further work, however, would be needed to put this correlation on a firm basis and to elucidate its significance.

Very remarkable aggregations of *N. stoliczkae* were observed in the stream that flows through the Nyag-tzu valley into the eastern end of Pang-gong Tso. The stream is small, with frequent small pools and holes in its course. In the shallow, more rapid reaches, no animals of any sort could be discovered. In the upper part of the stream, *N. stoliczkae* was taken in small numbers in pools cut off from the main channel. At about 4724 m., a skull of an Ammon sheep was observed lying in a pool-like expansion of the stream. Around this skull a very large number of specimens of Nemachilus had collected. It was supposed that the fish had aggregated around the skull to scrape organic matter from its surface, the food supply of the stream being obviously deficient. Later, however, at Nyag-tzu, alt. 4603 m. another even larger aggregate was observed. Here an estimated number of between one and two hundred fish were lying close together around a large stone on the bottom of a hole in the stream. Both sexes were present. It seems from the nature of this aggregate, that though a solid object forms a nucleus of aggregation, such behavior is not determined by the presence of an especially rich source of food. Hora *(in litt.)* writes that he has observed such aggregates of both Nemachilus and of Garra, and that he considers them to be, at least in part, expressions of breeding behaviour, though in his cases, but not in mine, a spacial restriction, the low water level in summer, may have been involved.

No cestode parasites were observed in any of the rheophil species of Nemachilus, but Datta (1936) records *Neoechinorhynchus rutili* (Müller) from *N. stoliczkae* from pools at the head of the Nyag-tzu Valley (L64).

[4] This may be a stream from which previous investigators have obtained *N. stoliczkae* (Hora and Mukerji, 1935).

In contrast to the part played by the tapeworm Ligula in the biology of the lacustrine species of Nemachilus, the Acanthocephala are probably not abundant enough to play any great part in the ecology of their hosts.

THE SPECIES OF LARGE STREAMS

Dyptichus maculatus and *Schizopygopsis stoliczkae.* Although both *Nemachilus stoliczkae* and *N. gracilis* are recorded from large streams, notably L37, between Tangtse and Mugleb, by far the most important members of the fish fauna of such localities are the Schizothoracine "snow-trout," *Dyptichus maculatus* and *Schizopygopsis stoliczkae.* Both species may co-

FIG. 4. A large torrential stream, L31 Lhabaps. The only species of fish present is *Dyptichus maculatus.*

occur in enormous numbers, as in the lower part of L37, just above Tangtse, or in L47, the stream that flows past Chagra and Phobrung into the northwestern end of Pang-gong Tso. There is, however, ample evidence that the range of environments suitable to the two species is not identical. *Schizopygopsis stoliczkae* is found not merely in large clear rapid streams, but also in the turbid waters of the Indus, both at Leh and at Yalapuk, and the species was brought me from the western end of Tso-nyak. Outside the area under consideration, a form of this species has been recorded from the delta of the Helmand in Seistan (Annandale and Hora, 1920). It can therefore clearly live in still water and must be regarded as rheophil rather than

rheobiont. *Dyptichus maculatus* on the other hand would appear to be a strictly rheobiont fish, as has been pointed out by Berg (1932). It was observed in six localities, L12, L15, L31, L34, L37, and L46. Of these L12, L31 (Fig. 4), and L34 may be regarded, at least in part, as torrential, though in all cases the species appeared to occur most abundantly in holes in the stream bed. The most instructive locality was L37, between Tang-tse and Mugleb (Fig. 5). Here Dyptichus was only noted in the lower half of the reach investigated, where there are many large stones in the course

Fig. 5. A large, moderately rapid stream, L37, half way between Tangtse and Mugleb. The reach photographed is at about the upper limit of the region inhabited by *Dyptichus maculatus*. *Schizopygopsis stoliczkae* in great abundance, breeding, *Nemachilus stoliczkae* and more rarely *N. gracilis*.

of the stream, which flows in a rather narrow valley and in consequence has rapid races not found in the upper part of the reach, where the stream meanders in a wide valley and where large boulders are rarer. It appears from this case that where a stream becomes sufficiently quiet, *D. maculatus* is unable to flourish, though *S. stoliczkae* may live and breed in great abundance.

Both *Dyptichus maculatus* and *Schizopygopsis stoliczkae* have a well developed exposed horny covering to the lower lip and both feed by scraping the surfaces of stones and rocks. Algae, including benthic diatoms, and insect larvae are the most important food materials obtained in this way.

Some sand is inevitably included in the alimentary tract by this method of feeding, but it is probable, from the uniform nature of the gut contents of certain individuals practically nothing but trichopterous pupae in one Schizopygopsis, masses of Cladophora and little else in one Dyptichus, that considerable choice is exercised in the selection of the surface to be scraped. In this the two fishes under consideration are probably more selective than is Oreinus.

Parasites probably play little part in the ecology of these fishes in running water. *Neoechinorhynchus hutchinsoni* Datta occurred in *Dyptichus maculatus* from Leh, and *Acanthocephalus kashmirensis* Datta in *S. stolizkae*

FIG. 6. Suru River at Kargil. (K88). *Ptychobarbus conirostris* and *Oreinus sinuatus.*

from L37, but were not common. In localities in connection with still water, *Schizopygopsis stoliczkae* may be infested with the common fish cestode *Ligula intestinalis* (L.); specimens were obtained from this fish living in the stream at the west end of Pangur Tso. They had presumably swum up from the lake.

THE SPECIES OF RIVERS

Schizothorax, Ptychobarbus and Oreinus. The deeper turbid rivers, exemplified by the Indus and the smaller Suru (Fig. 6), although the first contains at least *Nemachilus gracilis* and *Schizopygopsis stoliczkae*, differ

from the clearer large streams in lacking Dyptichus and in possessing a number of species never present in either the large or the small streams already discussed. Of these additional species, the two most important are *Oreinus sinuatus* and *Ptychobarbus conirostris,* but a number of members of the genus Schizothorax have also been recorded from the Indus by various authors.

Ptychobarbus conirostris appears, in Indian Tibet, to be an essentially rheobiont species found only in rivers. Specimens were obtained in the Indus at three stations as well as in the Suru. It is apparently a bottom feeder, living primarily on insect larvae, and although there is usually a certain amount of mud and sand present in the gut, such material is never found in the large quantities usually present in the gastro-intestinal tract of Oreinus. It is probable, therefore, that this species selects its insect food from the bottom, but unavoidably takes in some inorganic material with its prey, which is small compared with the size of its mouth. An as yet undetermined nematode is abundant in the alimentary tract of this fish.

Oreinus sinuatus appears to have identical habits in Indian Tibet and in Kashmir. It may be regarded as essentially rheobiont, the only specimen contradicting this being one from a large pond south of Chushol, regarded by Mukerji as a hybrid, *O. sinuatus* x *Schizothorax labiatus.* Neither parent occurred in the vicinity, and as I recorded this specimen in the field as Schizothorax and was quite familiar with the hybrids at that time, I cannot help suspecting that labels became interchanged during the transportation of the specimens. The food of *O. sinuatus* in Indian Tibet is essentially as in Kashmir, large amounts of mud being ingested. No parasites have been recorded from the material in the present collection.

Less characteristic than these two species are the various members of the genus Schizothorax. In the notes sent to Dr. Hora and used by him in the ecological observations in the report on the fishes collected by the Netherlands Karakorum Expedition (Hora and Mukerji 1935), I considered the genus as characteristic, not of the Indus as a whole, but of those regions such as the reach above Spithug, where there are extensive marshy fields and some small backwaters. However, Vinciguerra (1930) has recorded *S. esocinus, S. longipennis, S. Dainellii*[5] and an undetermined species from the Indus in Skardu, where the river valley appears to be narrow and without backwaters. It is more than probable that some species (*S. esocinus, S. labiatus* and *S. longipennis)* occur throughout the entire upper Indus and that others, notably *S. micropogon* and *S. planifrons* in Kashmir, and *S. tibetanus* in the upper parts of the Pang-gong depression, are more limnadophil and are found chiefly in still or slowly moving waters. No generalisation, therefore, can be legitimately made as to the requirements of the genus as a whole, except that in Indian Tibet it does not inhabit any flowing water save the large rivers. This is in accord with Zugmayer's conclusions, based

[5] This supposed species probably belongs in the hybrid series Schizothorax x Oreinus, though it differs from the hybrids figured by Hora (1934) and by Mukerji (1936) in certain respects.

on considerable experience in Turkestan and western Tibet, that the genus "ein Bewohner der Seen und grossen Flüsse ist, sodass das zentrale Tibet mit seinen Salzseen und kurzen Wasserläufen für ihn kein geeignetes Gebiet sein kann."

LIMNADOPHIL AND LIMNADOBIONT FISHES OF INDIAN TIBET

From the standpoint of their fish fauna, the lakes (Hutchinson 1937) investigated in Indian Tibet may be divided into three categories.

(a) Fishes apparently absent.

Ororotse Tso, Khyagar Tso, Midpal Tso, Tso Moriri and Tso Kar.

The absence of fish in Ororotse Tso may be more apparent than real. The lake seems to have a perennial ice cover that made collecting difficult, but in spite of this its plankton and benthos are quantitatively rich and would provide ample food for any fishes that could establish themselves. The low temperature would hardly be a barrier to *Nemachilus stoliczkae*, and it is possible that this species may occur in the lake; more probably the very steep valley of the effluent leading into the Chang-chenmo, which proved impassable for our caravan, has effectively prevented colonization of the lake.

The absence of fishes in Tso Kar is readily comprehensible for this lake is extremely saline and contains only halobiont forms such as Artemia. The other lakes, though slightly saline and alkaline, are certainly not sufficiently concentrated to exclude fishes altogether. The case of Tso Moriri is most interesting. Although *Nemachilus microps* and *N. stoliczkae* are recorded from its drainage basin, no fishes are known from the lake. A very favorable area, carpeted with Potamogeton, and comparable to the western end of Pangur Tso, exists where the Yan, the northern affluent of the lake, enters at Peldo-le. A small trawl was used on this area, but it yielded absolutely no fishes of any kind. It seems certain, therefore, that this lake does not possess a fish fauna comparable to that of Pangur Tso.

(b) Rheophil forms only present.

Yaye Tso, Sta-rtsa-puk Tso.

Yaye Tso yielded *Nemachilus stoliczkae*. All specimens were very young. In Sta-rtsa-puk Tso, *Nemachilus gracilis* was common while *N. tenuicauda* (Steind.) occurred in one of the pools of the marginal marshy area, which was doubtless connected with the lake earlier in the season.

(c) Limnadophil and limnadobiont species of Nemachilus with a functional swim-bladder present, with or without species of Schizothoracinae.

Pang-gong Tso, Tso-nyak, Pangur Tso, Tsar Tso.

These four lakes and some pools in their vicinity are very different in their fish fauna from the preceding localities. *Nemachilus deTerrai* Hora was obtained abundantly in a lagoon, separated from Pang-gong Tso by a narrow bar, at Man. A single specimen, almost certainly of this species,

was seen in the lake near Man; it may have been washed from a lagoon during a storm; fishes are clearly very rare in the lake itself. According to the inhabitants of Span-mik, west of Man, only a few small fishes occur in Pang-gong Tso; doubtless this statement refers to stray specimens of *N. deTerrai.* Zugmayer (1910) believed fishes to be entirely absent. At the northwestern end of the lake, in a pool in the swamp below Lukong, a specimen of *N. hutchinsoni* Hora was obtained. This species also occurred in Tsar Tso, a tiny weedy lake on the road between Mugleb and Pang-gong Tso and in pools near Tang-tse.

From Tso Nyak, which I was not able to visit personally, Sod-nam Tergas and Tzewan Tashi, two excellent Ladaki collectors, brought me *Nemachilus panguri* and *Schizopygopsis stoliczkae,* while the former species was very common in Pangur Tso and both species were obtained in a small rapid stream entering the western end of the latter lake. It must not be forgotten that *Schizothorax tibetanus* Zugmayer was described from one of the upper Pang-gong lakes and certainly belongs to the same fauna.

The problem of the occurrence of these interesting fishes, in one restricted part of the region investigated, raises many questions. Ecological notes on the species in question may first be given, followed by a discussion of the significance of the distribution of these fishes.

Ecology of the "Diplophysoid" Species of Nemachilus

The three species under consideration belong to a group *(Diplophysa auctt.)* of the genus Nemachilus, believed by Hora to be polyphyletic in origin, which are characterised by possessing a large functional swimbladder and by having the long dorsal lobe of the tail fin, which reaches beyond the ventral lobe. Such structural characters undoubtedly fit these fishes for life in relatively deep quiet waters, and the majority of records of such species, which are very characteristic of the Central Asiatic fish fauna, are from lakes or from streams in their immediate vicinity.

N. hutchinsoni. All the records of this species are from standing water, but in three cases it occurred in tiny pools a few meters in diameter and less than half a meter deep. The fourth locality, Tsar Tso, is also shallow, but is a more or less permanent lakelet, filled with a narrow leaved Potamogeton. The species may be regarded as limnadobiont, but in its known habitats can have little opportunity for vertical movement.

In view of the small size of the habitats of this fish, wide ranges of very variable and often high temperatures may be expected. The locality L36, a small pond between Durbuk and Tangtse, had a temperature of 23°C, in the late afternoon of July 26, 1932, but it not improbably froze at night. On June 27, the temperature of Tsar Tso lay between 12.5° and 14.5°.

The three small pools inhabited by the species were not studied chemically, but are certainly fresh; Tsar Tso shows slight traces of the accumulation of salt and alkali characteristic of the closed basins of the region, but

is much more dilute (alk. reserve 0.0015 N, Chloride 0.00155 N, pH 9.3) than are the larger closed lakes (Hutchinson 1937).

The single specimen from the pool at the northwest end of Pang-gong Tso yielded the cestode *Ligula intestinalis* (L.) (Datta 1936).

N. deTerrai. This species was only obtained from a lagoon in a drowned valley, cut off from Pang-gong Tso, just east of Man. The lagoon contained a good deal of water-weed, a narrow-leaved species of Potamogeton, probably *P. pectinatus.* The only adult specimens were obtained by Dr. de Terra, who found them floating dead at the surface of the water. Some of them had injuries on the skin, others were in perfect condition. It is probable that the injuries were due to still living fish feeding on those recently dead, and that the whitish material noted by Hora in the guts of some specimens was derived from this source. Later a few young individuals were obtained from the lagoon with a hand net. Though the water of the lagoon is about ten times fresher than that of the lake, it is distinctly alkaline and saline (Alk. reserve 0.0044 N., Cl 0.0076 N., pH over 9.6); all the alkali appeared to be present as carbonate (phenol-phtalein titration 0.0022 N.) It is not unlikely that the mortality of the adult fishes was due to an excessive rise in the alkalinity due to photosynthesis; Hora points out that supersaturation with oxygen cannot have caused death as there is no trace of the "gas-eye" condition, but it is known that in some fishes a high external hydrogen ion concentration may inhibit the respiratory movements of the branchial region (Willmer 1934).

There is little doubt that fishes of this species sometimes find their way into the lake itself; a single Nemachilus observed in the lake at Man, but unfortunately not captured, probably came from a lagoon, the wall of which may have been partially broken down by a storm. The complete absence of higher vegetation in Pang-gong Tso must make this lake a far less suitable habitat for fishes than the lagoon already discussed.

Hora indicates that one of the specimens retained in Calcutta is greatly distended by parasitic worms; this presumably refers to *Ligula intestinalis.*

N. panguri. This species is very closely allied to the preceding, and further work may indicate that they are synonymous. It evidently occurs in considerable abundance in both Tso Nyak and in Pangur Tso, though since it enters the small rapid stream at the western end of the latter lake, it should be regarded as limnadophil rather than strictly limnadobiont. In Pangur Tso this fish can be observed in great numbers swimming among the weeds at the western end, and a number of specimens were obtained in a very distended or broken condition at the surface, as a result of a heavy infestation with *Ligula intestinalis.*

At least that part of the population that inhabits Pangur is not subjected to such high summer temperatures as are found in the small pools inhabited by *N. hutchinsoni.* The temperature of the surface of the lake varied

from 14.13° to 15.05°C on August 13 and 14, 1932. The oxygen content on the former date was 5.4 mgrms. per litre. The lake is more alkaline but less salt (Alk. Res. 0.061 N., Cl, 0.0017 N., pH 9.6+) than Pang-gong Tso. This chemical difference, together with the much greater amount of shallow water, at least at the western end of Pangur, is probably responsible for the large amount of littoral vegetation that presumably provides good food and cover for the fishes. The water of Tso Nyak is probably fresh, though the presence of *Brachionus plicatilis* (Müller) in the plankton of the western end of the lake (Edmonson and Hutchinson 1934) suggests that an analysis would be desirable. Both Zugmayer (1910) and Sven Hedin

Fig. 7. Region inhabited by diplophysoid species of Nemachilus. The solid lines indicate the present hydrography; the broken lines the approximate hydrography at the time of the highest level of Lake Schlagintweit.
1. Habitats of *Nemachilus panguri*, 2. habitat of *N. deTerrai*, 3. habitats of *N. hutchinsoni*.

(1907, p. 311) note water plants in the upper Pang-gong Lakes and information received from my collectors suggests that the dark color of these weeds is responsible for the name Tso Nyak (Black Lake), which in spite of Sven Hedin's statement to the contrary, does seem to be used (Hutchinson, 1936) for the lake.

Physiography of the Region Inhabited by Diplophysoid Loaches

All the habitats of these three diplophysoid species lie within the drainage basins of large late glacial lakes (Fig. 7). It is very probable that all such species of Central Asiatic loaches, in which a functional swim-bladder is developed, are now found in regions, which, if not hydrographically connected with large lakes, were formerly covered by or connected with immense bodies of water in the later phases of the Quaternary Glaciation. As is pointed out below, the Pang-gong Valley was completely filled with

ice prior to the period of the high lake-levels, and subsequent to the latter has been isolated from Pangur Tso. *Nemachilus panguri,* now confined to these two isolated depressions, can only have originated, or at least have been dispersed, at a time when the region was wet enough and the lakes were at a high enough level for a hydrographic connection to have been established between them. The hypothesis may therefore be advanced that these diplophysoid loaches, although now sometimes found in rivers or in very small pools, in spite of their structural adaptation to life in still, deep water, are in a sense glacial relict species, derived from large lakes that have now shrunk or have entirely disappeared. The great development of the glacial lakes, however, does not distinguish the region in which the diplophysoid loaches of Indian Tibet inhabit from the other basins of that country in which no fish or only rheophil forms occur. All the closed basins of the western part of Tibet appear to have contained large dilute or fresh-water lakes at the same time. In one respect, however, both Pang-gong Tso and Tso Nyak on the one hand, and Pangur Tso on the other, differ from the other lakes studied in that they are members of chains of lakes. In the case of Pangur Tso the chain consists of only two members, Pangur Tso and a small unnamed lake, clearly marked on the survey of 1859, but never apparently described. Evidence that will be later presented suggests that this physiographic character of the region in question has provided a more continuously favourable environment than could be afforded by single lakes like Tso Moriri, or by the very shallow Sta-rtsa-puk-Tso.

The nature of the chains of lakes of the Pang-gong and Pangur Tso valleys has been illuminated by de Terra, who has shown (1934) that during the late Tertiary this area was crossed by rivers, flowing from west to east. "The third main drainage channel . . . followed the Nubra, Shayok, Tangtse and Harong valleys and continued via Chushol-Pangur Tso to the Tso Nyak. That the Pang-gong basin ever contained a large pre-glacial stream is doubtful. Being of *graben* structure, it probably had its individual drainage, which followed the eastward slope into Tibet." During the earlier phases of the glacial period this region was so heavily icebound that complete extermination of the fish fauna must be assumed. The widely distributed Schizothoracinae and hill-stream loaches would have been able to survive in the lower reaches of the rivers and in the lateral streams draining into such reaches, and it is also probable that more freshwater habitats were available in unglaciated parts of the Tibetan plateau than are today. On the other hand, any forms endemic to the basins in question are reasonably regarded as having originated since the maximum glaciation.

The Glacial Lakes of the Pang-gong Tso and Pangur Tso Basins

The most complete account of the various stages in the development of Pang-gong Tso is that of Huntington (1906). This account will be amplified and in some respects corrected by a later paper by de Terra, but is a

convenient point of departure. Huntington concludes that after maximum glaciation the Pang-gong basin held a small lake. A subsequent glaciation caused a considerable rise in the lake, the surface of which came to lie about 65 m. above the present water-level. The high-level lake so formed must have included Tso-nyak and the other modern lakes beyond the Tibetan border; as this large glacial lake is of some importance geologically and zoogeographically, I (1937) have introduced the name Lake Schlagintweit to designate it. At the eastern end, Lake Schlagintweit presumably received waters from a now dry lake described by Hedin (1907, pp. 250-252) while to the west it drained into the Tang-tse Valley (Huntington 1906, de Terra 1934) which itself contained a lake. The entire system therefore consisted of a chain of at least three lakes, running from about 80 kms. beyond the head of Tso-nyak, westward to Durbuk. De Terra (1934, see also Deevey 1937) formerly believed these lakes to have been of interglacial age, but now (personal communication) agrees with Huntington that they existed during a glacial (Third Himalayan Glacial) rather than an interglacial period. In view of the differences of opinion that have been expressed as to the age of these large lakes, the term Lake Schlagintweit stage is here used to express the condition of maximum lacustrine development in the latter half of the Quaternary Glaciation. It is reasonable to assume that this maximum development occurred simultaneously in both Pang-gong and Pangur valleys.

No published information appears to exist relative to the Pangur depression, but observations made when I visited the lake, together with determinations of levels made by Khan Sahib Afraz Gul Khan, make possible some reconstruction of its history.

The valley floor immediately to the west of Pangur Tso is covered by ancient lake deposits, rich in molluscan shells and plant debris and essentially similar to those found in deposits of the Lake Schlagintweit stage between Pang-gong Tso and Lukung. These deposits occur along the shores of the present lake and appear to be at least 20 m. thick. The sides of the valley in which the lake lies are dissected by numerous subsidiary valleys, from the lower ends of which large fans of outwash radiate. Between the fans a series of four rock-cut terraces is visible (Fig. 8), but wherever the apices of the fans reach a sufficient elevation, these terraces are obscured by outwash. The highest terrace lies at 4395 m. or 66 m. above the present lake surface; they therefore represent a rise in lake level of the same order as that which produced Lake Schlagintweit in the Pang-gong Valley. This high lake in the Pangur Valley was, from the absence of calcareous deposits on its terraces, certainly fresh, and can only have discharged its waters to the west towards Chushol and so into the drainage basin of Lake Schlagintweit. Such a hydrographic connection is confirmed by the presence of *Nemachilus panguri* in both Pangur Tso and Tso Nyak.[6]

[6] Certain very high terraces at Takung, which formerly (1936, 1937) led me to suspect that Pangur Tso might have been included within Lake Schlagintweit, are, as Huntington (1906) has pointed out and de Terra has confirmed verbally, not of lacustrine origin.

Subsequent to the Lake Schlagintweit stage the lake level fell in both basins. Huntington found evidence that Pang-gong Tso sank to a level below its present height. During later glacial advances a new rise in Pang-gong Tso occurred, but the lake did not reach such high levels as during the Lake Schlagintweit stage. Similar changes occurred in Pangur Tso. Here a series of four beaches is visible, cut into the lacustrine deposits of the earlier lake. The highest of these beaches lies at 4345 m. and indicates a rise of 16 m. above the present level, again commensurate with the corresponding rise in Pang-gong Tso. This beach lies just above a white band which presumably implies that the lake was mineralised; in any case it must have lacked an outlet.

FIG. 8. Pangur Tso from a point on the south shore near the western end of the lake. Note the four high level beaches (indicated by arrow) covered by the apices of alluvial fans, and the low beaches a little above the present water level. *Nemachilus panguri* abundant.

Since the second high-level period, a number of minor changes in level have occurred, and it is clear that the climate of the whole region has undergone continual cyclical fluctuation. This fluctuation has probably had little effect on the terrestrial and the rheophil aquatic fauna. Deevey's (1937) work clearly shows that the vegetation at the time of the Lake Schlagintweit stage was essentially similar to that of today, but it is certain that the altitudinal limits of the different vegetation zones must have lain lower. To aquatic species endemic to restricted regions, climatic changes of small amplitude may prove critical, because if the habitats are for a time unsuit-

able, there is no chance for the species in question to retreat and to advance when conditions again become favourable. It is therefore desirable to examine the available evidence relating to climatic change in post-glacial times.

Post-glacial Climatic Variation

a) Evidence from lake-levels. The most important, and indeed the only indisputable, evidence of post-glacial periods drier than the present, is derived from observations of lake-levels. These have been discussed in detail by de Terra and Hutchinson (1934). There are ample records that indicate a general period of low levels about 1860, and suggestions of a general periodic fall and rise of Pang-gong Tso, the whole cycle from one high level to the next taking rather over a century. Of even greater importance is Godwin-Austin's observation of a beach about 3 m. below the lowest 19th century level, i.e. between eight and nine meters below the 1932 level. If such a fall in level were general, much of the western end of Pangur Tso must have been dry, while the water in lakes as shallow as Tso Kar and Sta-rtsa-puk Tso must have disappeared entirely.

b) Additional evidence of a wide-spread post-glacial dry period is probably provided by some observations on the upper limit of agriculture. Huntington (1907 pp. 53-54), commenting on the supposed occurrence in Baltistan of large trees lying dead at an altitude greater than that at which even stunted trees now grow, writes "Probably the trees are relics of the dry epoch during the first half of the Christian era, but this has not been proved." Unfortunately the final statement made by Workman and Workman (1905) on the occurrence which provided the factual basis of this suggestion, does not give unequivocal evidence of any former extension of the tree-line in the Chogo-lungma Valley though possibly the average size of the trees was once greater, which possibility admits of more than one interpretation.[7] On the other hand, evidence does exist that in parts of Indian Tibet the upper limit of cultivation was at a greater altitude than it is today. The highest cultivated land at the present time is at Korzok, on Tso-Moriri in Rupshu, where a little barley is grown between the village (alt. 4556 m.) and the lake (alt. 4528 m.); at Phobrang, northwest of Pang-gong Tso, there is also a little cultivation (alt. 4528 m.). Yet Francke (1914 p. 54) writes, "As I was told by another man from Rubshu, there are ruins of ancient settlements and watercourses all over the country. They are found on high hills in Rubshu, and are ascribed to a tribe of Mon, the pre-Tibetan inhabitants of the country. These Mon must have been marvels of endurance. How they could have cultivated fields at those altitudes is a mystery. The barley fields of the bKor-rdzod monastery are in Mr. Drew's opinion the highest in the world. But those of the Mon settlers must have been higher still. . . . It may sound incredible that there should have been fields still higher than the present fields of bKor-rdzod whose harvest sometimes fails.

[7] "Prostrate cedar trunks much larger than any of those now standing. . . . Both these and the growing cedars ceased at about . . . 12,679 ft." (F. B. and W. H. Workman, 1908. Pp. 76-79.)

But I remember that also on one of my former journeys, in Zangskar, I came across the ruins of a Dard settlement at an altitude where it was icy cold even in summer." Although the possibilities of agriculture in this region are limited largely by water supply and by presence or absence of suitable sites for fields, it is improbable that the present altitudinal limit is set by these factors, seeing that practically the whole of the water supply of the modern settlements comes from snow and ice on the mountains and local precipitation is probably of negligible importance in agriculture, while level sites are available, as at Chagra above Phobrang, at altitudes slightly in excess of the present limit of cultivation. It is therefore clear that if the limit of agriculture was formerly higher, conditions for the ripening of the crop, now often cut when partly green, must have once been more favourable. This, like the supposed, but unproved, upward extension of the tree line, would seem to point to a warmer, drier period, presumably some time during the first half millennium A. D.

c) Patination of engraved rocks. Some evidence of climatic change is afforded by the numerous engraved rocks that occur throughout the lower part of the region studied. It must be admitted that the interpretation of this evidence is open to many difficulties; my earlier views (Hutchinson 1936) differed somewhat from the more mature if less informative standpoint of the present paper.

Hawkes, Hawkes and de Terra (1934) have described "a flake of greenish-black trapp, covered with a thick reddish-ochreous patina," picked up on the third terrace above the Suru river at Kargil. "In its original form it may certainly be attributed to the great family of Palaeolithic flake industries. . . . A Lower Palaeolithic date would seem to be indicated." After the formation of the patina the whole flake was retouched, converting it into a square-ended scraper, "that might be Upper Palaeolithic or Neolithic" (p. 8). Later in their paper they remark, "The period in which the patina was laid on . . . may belong to a last interglacial or a dry post-glacial time." A limonitic cement, present in the gravels of the Kargil basin, is also attributed to the same period. If the specimen be taken at its face value, it is clear that no patination can have occurred on the surface of the Kargil terraces in recent times. Though it is admittedly possible, there is unfortunately no evidence that the artifact had lain on the same surface since the Neolithic period. Traces of presumably post-Neolithic rock engravings in the vicinity appear to be well patinated.

Not far from Kargil, on the treaty road above Shimsha Karbu, is a well-known rock, covered with rock-engravings. The oldest represent stupas and other symbols, as well as a few carvings of ibex. These engravings are somewhat patinated and cannot antedate the introduction of Buddhism to the country in the 8th century. The greater part of the rock is covered with engravings of ibex, quite unpatinated, and in part superimposed on the older series. According to Francke, who figures the engravings (1914),

the ibex is associated with a fertility cult of pre-Buddhistic origin. It is clear therefore, that the numerous engravings of the animal in Indian Tibet may be of various ages, and, taken by themselves, their patination gives no indication of climatic changes. The partially patinated state of the engravings of stupas, however, shows that in the country in the vicinity of Kargil, the agencies that produce patination have been able to act, at least in isolated localities, at some time subsequent to the 8th century A.D. The significance of the Kargil artifact is, therefore, rather problematic.

Close to the village of Tang-tse and therefore within or very near to one of the basins of the great interglacial fresh-water lakes of the Lake Schlagintweit complex, is another engraved rock, of the greatest interest. The rock has been described by Francke (1925) and F. W. K. Müller (1925) on the basis of photographs sent from the Moravian Mission at Leh. Their descriptions are not quite complete, as they had no information relating to the western face of the rock. Some supplementary observations made in 1932 can therefore be added to their account. I am much indebted to Mons. E. Benveniste and Professor Silvain Levi who have examined my photographs and notes.

The Tang-tse rock is a large cubical mass of Ladak Granite, the surfaces of which are covered with a rich brown desert patina. In places, this patina has flaked away and no new patination appears to be taking place. In some parts of Indian Tibet, noticeably between Chushol and Pangur Tso, all the granite boulders give an appearance of having lost their patina; it must, however, be admitted that the most intense patina is found at the bottom of valleys, in closest proximity to whatever sources of water may have existed under the conditions accompanying its formation, so that such unpatinated rocks may never have had patination. The rock at Tang-tse is engraved on three faces. On the west face, there is a short Tokharian inscription, read by Professor Silvain Levi as *"tane wewimaruśasi"* the meaning of which is problematic. Below it, less deeply incised, and so apparently, though not actually, somewhat patinated, is a single Chinese character. At the end of the Tokharian inscription is a large cross patée. On the south face is a long Soghdian inscription partially read by Müller, recording the journey of a man from Samarkand towards Tibet. There is also a large cross and what appears to be the name Jesus on this rock face. The letters are deeply incised into the white granite and no patination whatever has taken place since they were engraved. The extreme whiteness of the inscription is so remarkable that Francke relates that he inquired of the missionaries who sent the photographs as to whether the inscription had not been chalked prior to photography. I examined the inscription very carefully, and am quite convinced that it has not been tampered with. Since the two Christian inscriptions must, on historic and linguistic grounds, be early medieval, it is clear that no patina has formed at Tang-tse in the last half millennium.

On the east side of the rock a number of engravings of animals, hunters, mchod-ten and other Buddhistic symbols are to be observed. The most remarkable of these engravings are the representations of two stags, apparently pursued by men with slings. Men with bows and arrows, hunting a yak, and several figures of ibex, are also depicted. Francke points out that the stag does not now occur in this region, and that the wild yak is not found today nearer than the Upper Changchenmo. Dr. de Terra and I observed two fine specimens grazing in a small lateral valley at Nying-ri. The wild yak, however, has probably been exterminated in the upper parts of the more settled valleys within historic times. The case of the stag is more difficult to explain. The genus Cervus in Northern India is at present restricted to the forested regions of Kashmir, where *C. hanglu* Wagner is found in the Kashmir Valley, part of the Kishen-ganga Valley and in the Kishtwar district. Eastward of the range of this species, *C. w. wallichi* Cuvier occurs in the wooded country south of Lake Manasarowa. As far as I can judge from the Tang-tse engravings, the stags represented are *C. hanglu,* the antler being five-tined and the apical tines being sub-equal. *C. hanglu* is said (sub *C. cashmirianus* Fitzinger) by Lydekker (1898, on the authority of Percy), not to cross the Zoji-la, so that at the present time it never appears to leave the well-watered forests on the southern slope of the main Himalayan range, at least two hundred kilometers in a straight line from the engravings and considerably more by any possible track. If the representation at Tang-tse was supposed to depict stag-hunting on the Kashmir side of the range, it is curious that no other engravings of stags are to be found in Indian Tibet, particularly in the region nearer to the present home of *C. hanglu.* While the even more remote possibility that the scene depicted represents Turkis hunting *C. yarkandensis* Blanford must be borne in mind, the most reasonable interpretation of the engraving seems to be that at some period in the early middle ages Indian Tibet was damp enough to support more flourishing thickets of trees in the valleys than exist at present, and that some colonies of the Kashmir deer were able to establish themselves in the country.

Laudermilk (1931) has summarized existing knowledge as to the cause of desert patina and concludes that this type of surface alteration is organogenic. In most cases a lichen appears to be responsible, though in the beds of streams algae may be the causal agents. It is clear that the patina is not produced in either humid or exceedingly arid regions, but it is characteristic of the less extreme type of desert in which there is well-marked but seasonal precipitation. I am inclined to think that the absence of patina on the surface of the Soghdian inscription at Tang-tse implies that the Tang-tse Valley has been drier in post-medieval times than it was prior to the visit of the man from Samarkand. On the other hand, the rock at Shimsha Karbu and possibly the stags on the rock at Tang-tse suggest wetter con-

ditions, leading to patination in the former case, in the middle ages, certainly subsequent to the beginning of the eighth century A.D.

Summarizing the above observations on the limit of agriculture and on patination, it is clear that quite apart from the variations in the level of the lakes, evidence exists that points to both wet and dry periods in Indian Tibet during post-glacial time.

Limitation of the Distribution of Diplophysoid Species of Nemachilus

The hypothesis having been advanced that the species of Nemachilus with functional swim-bladders are relict forms originally characteristic of the great lakes of the third Himalayan glacial, it remains to consider why they should now in Indian Tibet be restricted to the lakes of the Pang-gong and Pangur valleys.

Although the general condition of the country is certainly much drier than during the Lake Schlagintweit period, ample evidence has been presented above to indicate that desiccation has been an irregularly cyclical phenomenon, and that although periods drier than today are more difficult to establish than are wetter phases, indications of such extremely arid times are by no means lacking. In such dry periods populations of lake fishes would be exposed to even more unfavourable conditions than may operate upon them today.

If we suppose that originally a species of loach with a functional swim-bladder lived in the lake that formerly filled the Tso Kar depression, there would be little chance of it surviving in Sta-rtsa-puk Tso until today, because a period dry enough to produce the lowest submerged beach of Pang-gong Tso would certainly cause the disappearance of the shallow modern lakes in the Tso-Kar basin. Corroboration of this is afforded by the fact that although many molluscan shells can be found in the deposits of the glacial lake of that depression, none are now living in the weedy Sta-rtsa-puk Tso, which would appear to be a most favourable habitat for fresh-water gastropods. It is, however, unlikely that the valleys surrounding the desiccated lake would be entirely dry, and rheophil species might survive, nearer the snowline, in the head waters of streams that failed to reach the site of the lake.

A less extreme but equally important result of the lowering of the lake level might be felt in the case of Tso Moriri. It has already been pointed out that in Pang-gong Tso, the only habitat in which diplophysoid loaches occur in any abundance is a lagoon, and that in the open water of lakes such fishes seem to flourish only in the presence of abundant vegetation. In Tso Moriri such vegetation appears to be confined largely to the shallow water of the estuary at Peldo-le, and possibly in similar situations at the south end of the lake. If influent streams failed to reach the lake and its volume became reduced, the estuaries and weed banks would suffer

more than any other part of the limnetic biotop, and as the sides of the basin are steep, the best habitats of the fish would be destroyed by a relatively small fall in the water level (2-3 m.). This in itself might cause a great reduction or even extermination of the population. If such a change induced the remaining fishes to feed more on Copepods, the intermediate hosts of Ligula, as is quite likely, another unfavourable factor would be intensified, and in some localities it is possible that increasing concentration alone might reduce the viability of the fish. Such factors, destruction of feeding grounds, increasing concentration and possibly excessive parasitic infection, would probably operate in all the basins of Indian Tibet except those in which limnadophil loaches are actually found, and once the whole population became extinct, no opportunity for its replacement would occur. A fall in the level of Pang-gong Tso comparable to that recorded in the middle of the last century would almost certainly lead to complete desiccation of the lagoons and so to the extermination of the present precariously situated fish population. But however low the water may be in Pang-gong Tso, Tso Nyak certainly would provide a refuge for lake fishes, and the same is probably true of the small and presumably fresh-water lake to the east of Pangur Tso. Moreover, the morphology and chemical conditions of the latter lake seem to be more favourable for abundant vegetation than those of the other closed lake basins, so that some vegetation might survive a considerable fall in water level. Only in the case of the localities inhabited by *N. hutchinsoni* in the Tangtse valley does any apparent difficulty arise. This species is, however, clearly brought into small ponds by floods, and the drainage in the vicinity of Tsar Tso is so uncertain that during wet phases *N. hutchinsoni*, which will doubtless be found in the Tso Nyak region, probably has considerable opportunities of migration between the Pang-gong or even Tso Nyak and Tangtse valleys. Huntington indeed says that Tsar Tso overflows regularly, but unfortunately does not indicate into which valley its effluent normally runs. While the evidence presented is undoubtedly fragmentary, all of it points to the conclusion that only the exceptional physiography of the Pang-gong and Pangur valleys have allowed a true limnadophil fish fauna to persist through successive cycles of climatic change.

ZONATION, COMPETITION AND COMPARISON WITH OTHER REGIONS

The account already given of the distribution of the rheophil fishes of Indian Tibet indicates that, in a typical river system, these fishes are found in a rather regular order. The lowest element in such an ordered series of habitats, the turbid rapid river, might be expected to precede yet another member of the series, the slow, mature river with an essentially limnadophil fauna. Though the greater part of the region under consideration is physi-

ographically unsuited to the development of such rivers, indications of this type of habitat and fauna can be found both in the present work and in the literature of Central Asiatic ichthyology.

Although the upper part of the Jhelum was not examined, it is probable that at least some of the species found in Indian Tibet occur in the head waters and tributaries of that river. Near Srinagar, the Jhelum resembles the Indus at Leh in the presence of *Oreinus sinuatus* and *Schizothorax esocinus*. In the canals and lakes connected with the river and to some extent in the river itself, more limnadophil species have also made their appearance, the endemic *Schizothorax planifrons* and *S. micropogon* being the most important. Species of sub-Himalayan distribution belonging to groups not represented in Central Asia also occur in the Kashmir valley, of these *Crossochilus punjabensis* Mukerji is probably the commonest form in slowly moving water. There is, however, no indication that an invading limnadophil fauna has been able to displace the Central Asiatic species. At the present time any fishes entering Kashmir from the south and west would have to negotiate very rapid reaches in the Pirpanjal Mountains.

A similar development of a limnadophil fauna is doubtless indicated by Zugmayer's observations on *Schizothorax tibetanus* in the upper part of the Pang-gong depression.

Nikolski (1933) has studied the relation of the fish fauna to the rate of flow of the Amu-daria and the Chu. Both rivers originate near the northwestern margin of the Central Asiatic sub-region of Berg and therefore contains forms of wide Palaearctic distribution, not found in the greater part of Central Asia. The part of the Amu-daria investigated contained neither Schizothoracinae nor Cobitidae; *Schizothorax intermedius* and *Schizopygopsis stoliczkae* are however known from the upper part of the Amu-daria drainage system. Neither species reappears in the rapid reaches lower down, where the rheophil *Barbus brachycephalus* Kessler is common. In the river Chu, *Schizothorax pseudaksiensis* Herz. occurs commonly only in the upper part of the region studied (Stations 1-4, from 25 km. below Vassilievka to 15 km. below Uspenovka), where it formed 6-14% of the total catch. In this region the river is rapid with much suspended matter. The species disappeared below Novotroitzkoe (Station 9). With it are associated certain other rheophilic forms, *Capoetobrama kuschakewitschi* (Kessl.), *Leuciscus leuciscus* (L.) and *Nemachilus* (sub. *Diplophysa*) *dorsalis* (Kessl.). The latter disappears where the water becomes slower and less turbid at Station 9, but the other two species continue far down the river. The limnadophylic *Rutilus rutilus* (L.) overlaps the range of Schizothorax slightly; the other dominant limnadophils *Leuciscus idus* (L.) and *Abramis brama* (L). do not appear till Station 12-13 where the water is somewhat less turbid than at Station 9. At 35 km. above Guliaevka (Station 15) the river becomes very rapid over a short reach. Neither of the upper rheophiles of Central Asiatic origin reappear, but the three dominant

limnadophiles are absent, the dominant species here being *C. kuschakewitschi.* A little below this point the limnadophiles become dominant, and the rheophil species completely disappear, this part of the river becoming a typical "Abramidenregion." It is important to note that both *S. pseudaksiensis* and *N. dorsalis* are well known in Lake Issyk-kul itself.

Although in Kashmir and possibly elsewhere species of Schizothorax can contribute to the fauna of slowly moving rivers and lakes, Nikolski's investigations indicate that where limnadophil fishes of other groups can enter rivers containing Schizothoracinae, they tend to displace the Central Asiatic and doubtless fundamentally more rheophil elements in the fauna. It is most interesting that such elements should reappear in Issyk-kul itself, though it is well known that the littoral regions of large lakes may support a fauna more characteristic of lotic localities than that found in sluggish rivers.

The zonation that can be observed in the part of Southwest Central Asia under investigation may now be expressed in a schematic manner.

I. Headwater streams.[8] Nemachilus zone.
Rheophil species of Nemachilus, particularly *N. gracilis* and *N. stoliczkae*; and more rarely *Glyptosternum reticulatum.*

II. Large streams. *Schizopygopsis stoliczkae-Dyptichus maculatus* zone.
a. In least rapid reaches *Schizopygopsis* and *Nemachilus* sp. only.
b. In intermediate reaches Dyptichus, Schizopygopsis and Nemachilus.
c. In the most torrential reaches, only *Dyptichus maculatus.*

III. Rapid turbid rivers. *Ptychobarbus conirostris* zone. *Ptychobarbus conirostris, Oreinus sinuatus* and in parts of the Indus rheophil species of Schizothorax (*S. esocinus, S. labiatus,* etc.), though it is possible that the last genus represents a rather more mature stage in the series than do *P. conirostris* and *O. sinuatus* when found by themselves. At least *N. gracilis* and *Schizopygopsis stoliczkae,* but not *Dyptichus maculatus,* occur.

IV. Slow rivers, lacustrine swamps and their channels and lakes. Zone of limnadophil species of Schizothorax. This zone is probably composite. In northwestern Central Asia it is replaced by a typical Abramis region, which it represents elsewhere. It is clearly best developed in Kashmir, where, however, groups of extra-Central Asiatic affinities are found. The species of Schizothorax most characteristic of the zone usually appear to be endemic to their basins. In at least some localities Schizopygopsis persists into this zone (Annandale and

[8] In presenting this scheme it must be pointed out that although the streams in group I are undoubtedly to be regarded as headwaters, little direct evidence exists of a complete passage from group I through group II to group III. Most of the small streams studied directly enter either the rivers or lakes, or as in the case of those near Leh, are now diverted for irrigation and fail to reach the Indus, at least in summer. It is, however, probable that the upper parts of streams of zone II are essentially like those of zone I. This is true, for instance, in the case of the Lukong stream, which was examined high up between Chagra and Togom Tso, at about 5,800 m, but contained no fish. It must therefore be remembered that although the complete scheme is theoretically possible and is not improbably realized in nature, the majority of the stations in zones I and II are at comparable hydrographic levels.

Hora, 1920). The "diplophysoid" species of Nemachilus are probably not to be regarded as characteristic, because they chiefly occur in lakes on the one hand, and in the rapid streams and rivers flowing into such lakes on the other.

Examining the scheme from a zoo-geographical standpoint, it is clear, as indeed is to be expected, that at least among the Schizothoracinae the species characteristic of the upper parts of the system are more widely distributed than those characteristic of the lower parts.

It is also noteworthy, that in passing from the headwaters, down stream, the transformation of the biocoenosis is for the most part additive, rather than substitutive, a situation that would seem to be characteristic of the fishes of the upper parts of river systems (Shelford, 1911). It is possible that considerable substitutive transformation occurs in passing from Zone III to Zone IV.

The scheme here put forward, primarily for Indian Tibet, enables the streams of that region to be compared ecologically with those of other parts of the world. Comparable classifications of the streams and rivers of Europe have been summarized by Thienemann (1926) and by Carpenter (1928). The European and West Central Asiatic zonation may be compared as follows, the enumeration of the former being that of Carpenter:

EUROPE		S. W. CENTRAL ASIA
A. Highland streams and rivers		
A1. Headwaters	I.	Nemachilus zone
A2. Trout-beck	II	*S. stoliczkae-D. maculatus* zone.
A3. Minnow-reach (Thymallus or Salmonid region)	III.	Ptychobarbus zone
B. Lowland rivers B1. Barbus region B2. Abramis region	IV.	Oreinus and endemic species of Schizothorax, the former dropping out and the latter becoming more important in lakes and lacustrine swamps.
C. Tidal region		Not represented.

It is highly probable that a division of my Zone IV is possible, and for this reason, and because the physiography of the region precludes a complete series of stages to the tidal region without rejuvenation of the river and a complete change in the zoogeographical nature of the fauna, I have preferred provisionally to indicate my zones by Roman numerals, rather than to adopt Carpenter's excellent scheme.

Instructive comparison can be made with the alpine streams of Europe; for this purpose Thienemann's (1936) recent study is valuable. It is at once apparent that not only are my maximum temperatures higher and ox-

ygen contents lower than in the streams of Upper Bavaria, as indeed is to be expected, but that only a small proportion of my stations (the torrential streams of IIc) are to be regarded as typical of high mountain areas. The very productive streams at Chagra and Lukong are clearly comparable to Thienemann's intermediate type (II Übergangsbäche); most readers will be familiar with similar streams, in any but the flattest landscapes, and at no great altitudes. In the case of these two examples, the low gradient can be explained by the structure of the Pang-gong depression and of the valley to its west, various geomorphological factors dependent largely on retention of the remains of mature pattern doubtless operate in other parts of the region (de Terra, 1934) in reducing the abundance of young and typically mountain torrents. Torrential streams, however, are doubtless much more characteristic of the southern Himalayan slope; and indeed Hora (1930, 1934) has indicated how retrograde evolution of the suctorial mechanism of *Glyptosternum reticulatum* has occurred as the result of life in the "less turbulent waters of the Highlands of Central Asia." *Dyptichus maculatus*, alone of the fishes of Indian Tibet, would seem to be strictly dependent on the mountainous nature of the terrain.

Finally, it is possible to compare the more complete zonation in Indian Tibet with the conditions prevalent in Chitral, from which region Hora (1934) has reported an important collection made by Chopra. This investigator obtained fishes at ten stations. In the largest river, the Chitral, clearly a habitat representing my Zone III, *Glyptosternum reticulatum, Schizothorax esocinus, S. labiatus, Oreinus sinuatus griffithii* McCl., and *Nemachilus choprai* Hora, occurred. This association is different from that of the Indus at Leh or of the Jhelum at Srinagar, but clearly represents a comparable cocoenosis, more closely resembling that of the former in its lack of any limnadophil species. In the smaller streams, which are comparable for the most part to those of my Zone II, but in the case of Chopra's Station 2, more closely resemble the localities of my Zone I, a fauna entirely different from that of equivalent stations in Indian Tibet is found. Dyptichus and Schizopygopsis are absent and are replaced by young specimens of *Schizothorax labiatus* and *Oreinus sinuatus griffithii.* Since very large numbers of fishes from large streams in Indian Tibet were examined, it is safe to conclude that in the latter territory neither Oreinus nor any species of Schizothorax regularly invade Zone II. We must therefore conclude that in Chitral absence of competition with Dyptichus and with Schizopygopsis allows the younger individuals of these two river species to wander far further up into the headwaters than they are able to do in Indian Tibet. Such limitation to particular zones in the presence of competitors of species which by themselves are more eurytopic, is not improbably an important characteristic of lotic systems. Striking cases in the triclad Turbellaria have been reported by Beauchamp and Ullyot (1932).

SUMMARY

1. The commoner Schizothoracinae (Cyprinidae) of the Kashmir valley may be classed as limnadophil, feeding selectively on water plants and invertebrates *(Schizothorax planifrons, S. micropogon)*, rheophil and carnivorous *(S. esocinus)*, and rheobiont, feeding on the bottom material *(Oreinus sinuatus)*. A few observations are made on other fishes found in this region.

2. The streams of Indian Tibet have higher maximum water temperatures and lower oxygen concentrations than streams at lower altitudes. The fishes of the region may be regarded as heteroeurythermal, *Nemachilus gracilis* perhaps more than others. The oxygen concentration never falls low enough to act as a limiting factor. The size of the stream, the rate of its flow and its capacity to produce food are probably the most important factors in regulating the distribution of the fish fauna.

3. The dependence of the fauna on the nature of the stream, independent of chemical factors and temperature, permits a schematic presentation of succession in an ideal river system as follows:

I. Headwater streams. Nemachilus zone.
Rheophil species of Nemachilus, particularly *N. gracilis* and *N. stoliczkae, Glyptosternum reticulatum* more rarely.

II. Large streams. *Schizopygopsis stoliczkae-Dyptichus maculatus* zone.
- a. In the least rapid reaches only *Schizopygopsis stoliczkae* and *Nemachilus* spp.
- b. In intermediate reaches, *Dyptichus maculatus, Schizopygopsis stoliczkae* and *Nemachilus* spp.
- c. In the most torrential reaches, *Dyptichus maculatus* only.

III. Rapid turbid rivers. *Ptychobarbus conirostris* zone.
Ptychobarbus conirostris, Oreinus sinuatus, as well as *Schizopygopsis stoliczkae* and *Nemachilus gracilis*. Dyptichus is absent. Rheophil species of Schizothorax *(S. esocinus, S. labiatus)* may be present.

IV. Slow rivers, lacustrine swamps and their channels, lakes.
Probably a composite zone, characterized by limnophil species of Schizothorax and fish from other zoogeographical regions entering the periphery of Central Asia, as in the Kashmir valley, where the zone is best developed.

Comparison is made with zonation elsewhere. Only the streams of IIc can be regarded as characteristic of high mountains.

4. Evidence is presented, from Chopra's collections made in Chitral, that where the characteristic species of Zone II are absent, young specimens of *Schizothorax labiatus* and *Oreinus sinuatus griffithii,* penetrate fur-

ther upstream, into Zone II or even into Zone I, than do the corresponding forms where the complete series of associations is developed.

5. Evidence is presented which indicates that the "diplophysoid" species of Nemachilus, with functional swim-bladders, in the Pang-gong and Pangur valleys, originated or at least were dispersed, at the time of the high-level Lake Schlagintweit (Third Himalayan Glacial). It is suggested that all the species of this group have had a like origin and dispersal. The available evidence as to post-glacial climatic oscillations is summarized; it is suggested that these "diplophysoid" loaches have survived in their present habitats, though absent from other lakes which had high-level stages, because post-glacial dry periods would render any lake unsuitable for such fishes unless it were directly connected with at least one other lake and were of sufficient depth.

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AN ECOLOGICAL STUDY OF WYOMING SPRUCE-FIR FOREST ARTHROPODS WITH SPECIAL REFERENCE TO STRATIFICATION

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INTRODUCTION

In an effort to determine the numerically prominent aestival arthropods of a subalpine spruce-fir climax forest habitat, and their relation to the stratification of physical environmental factors as controlled by the dominant vegetation, an investigation was conducted over an eight-week period during the months of July and August, 1936, in the Medicine Bow National Forest of Wyoming. This study maintained the quantitative viewpoint which marked the researches of McAtee (1907), Shelford (1913), Adams (1909), Beebe (1916), Wolcott (1918, 1937), Sanders and Shelford (1922), Weese (1924), Blake (1926, 1931), King (1927), Smith (1928), Shackleford (1929), Bird (1930), and Beed (1936), and the biotic community concept as expressed by Vestal (1914), Taylor (1927, 1935), Bird (1930), Phillips (1931), and Shelford (1931).

EXTENT OF STUDY

In this paper the attempt is made to point out some of the measurable factors of the physical environment and the composition of the endemic animal communities. Emphasis is placed: (1) upon the problem of stratification, i.e., the quantitatively and qualitatively determined vertical distribution of arthropods as correlated with the results of instrumental measurements of the factors of temperature, humidity, wind, and especially evaporation stress; and (2) upon the seasonal abundance of these forms in their respective strata and in the habitat as a whole, and its correlation with climatic changes as exhibited during the period of investigation.

As pointed out by Shelford and Towler (1925), communities must be determined by dominants, the limits of the dominants as such delimiting the communities; a dominant species being one which through abundance, size, or interaction with other organisms controls the environment. Obviously the trees are the dominant organisms of the spruce-fir forest habitat.

Since any biotic community must be largely considered as a unit (Shelford 1912a, 1931; Vestal 1914; Phillips 1931), it appears inappropriate to apply the term *dominant* or any of its derivations to both the trees of the forest and to ecologically important animals which appear therein. This view precludes in this study the use of the word *predominant*, suggested by Shelford (1926) "as covering all organisms of outstanding abundance or obvious importance." This term implies a precedence of the endemic animals over what appears to be, until otherwise demonstrated, a naturally pre-

cedent and dominant vegetation. Clements (Shelford 1926) has offered "the word *influent* to cover those organisms which have important relations in the biotic balance and interaction." This is a valuable term, but can accurately be applied only after the degree of importance of the various animal species in the biota is discovered. The mere determination of relative abundance, as carried out in this study, affixes to certain animals in the biota a numerical importance only. Such importance must not be considered as necessarily indicative of corresponding influent rank.

It appears desirable, therefore, to designate an animal species which is abundant in its given community by the term *prevalent*. This word means simply that the animal prevails in its community. It is introduced here as a temporary ranking applicable until the true biotic value is determined for the species concerned, and as a term usable in indicating species numerically important in the strata studied. The marked prevalence of any species within a given stratum suggests stratum choice on the part of that species (Shelford 1912a). This ranking was determined for each of the strata investigated in the spruce-fir forest.

This paper deals especially with stratum choice and apparent responses of the prevalent species to factor shifts. Only the prevalents will be considered here.

The terms employed to designate the strata especially considered in this paper do not in all cases agree with those used in earlier forest studies. These disparities are entirely due to the conditions within the forest studied, and not to any desire to change the terminology. Because of the shallowness of the litter layer, and the apparent unity of its population with that of the layer of duff below, the two are combined for purposes of study and designated as the litter-duff stratum. Because of the comparative scarcity of herbaceous growth and the abundance of the half-shrub, Vaccinium, the stratum in which the conditions were measured at 0.1 meter is termed the herb-half-shrub stratum. The absence of deciduous shrubs and the common occurrence of coniferous reproduction as the only undergrowth above the herb-half-shrub stratum necessitates the loose term of *undergrowth* stratum. Evaporation rate in this stratum was measured and collections of its animal population were taken at 1 meter above the forest floor. Evaporation measurement made at 3 meters, and sweep collecting done in the 2-3 meter level in higher coniferous reproduction and the low-hanging branches of old trees, constitute studies in the *low tree* stratum.

With the exception of a few species of flies, the arthropods collected in the above-ground strata appeared confined to the vegetation. In order, therefore, to picture clearly the conditions of distribution in the spruce-fir forest, the term *epiphytic* population will be used when referring to that above the forest floor. Likewise, *epiphytic* strata will collectively indicate the strata above the forest floor.

In order that as detailed an idea as possible may be gained of the habitat studied, considerable attention is given to an account of the vegetation.

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THE REGION

PHYSIOGRAPHY

The Medicine Bow Range is topographically a northwestern continuation of the Front Range of Colorado. A striking feature is the plateau-like structure of the main mass of the uplift. On its eastern flank it arises abruptly from the plains about 2,000 feet; then it slopes back almost at a level with an average elevation of 9,000 to 10,000 feet to the central uplift around Medicine Bow Peak, which is again about 2,000 feet above the plateau. This plateau-like portion of the range is 5 or 6 miles in width and

supports, for the most part, a comparatively abundant forest growth (Emmons 1902).

Geology

"The Medicine Bow Mountains consist of an immense uplift of Pre-Cambrian crystalline rocks of igneous and sedimentary strata, all of which have suffered more or less metamorphosis (Hallock 1931, Knight 1929). Eastward from the summits of the Snowy Range, granites, dolomites, schists, and gneisses may be successively observed (Ramaley 1907, Cary 1917)" (Hanna 1934). Throughout the greater part of the plateau the rocks are largely concealed by glacial drift and soil, the area studied overlying a northeast-southwest stratum of French slate.

Climate

The geographic and topographic relations of the subalpine forest formation serve to explain the boreal climate in which it thrives. This is characterized by a short growing season, relatively high precipitation, mostly in the form of snow (considerable of which remains on the ground throughout the greater part of the year), and wide diurnal and seasonal range of temperatures. The long winter is marked by high winds and excessive transpiration (Weaver and Clements 1929, Hanna 1934).

The last trace of snow in the immediate vicinity of the study station finally disappeared on July 4 (1936). Other snowdrifts were in evidence in the area for some days following this time. The writer was informed by Mr. Gilbert N. Hunter, Ranger of the Medicine Bow National Forest, that the autumn and winter winds in the Medicine Bow region are noteworthy for their high velocities.

No year-round meteorological observations have been made for the vicinity of the investigation, those of the University of Wyoming Summer Camp covering only the latter part of June, July, and much of August of each year from 1931 to 1936.

The summer rainfall of 1936 appeared to be unusual because of the excessive precipitation during the month of July. A four-year average (1933-1936 inclusive) for July rainfall at the University Camp is 2.06 inches. During July of 1936, this amount was nearly doubled, 3.73 inches being recorded, as shown in Table 5.

THE HABITAT

Location

In Albany County (Wyoming), Township 16 N.—Range 79 W., in the southeast corner of Section 14, and about 35 miles west of Laramie, is located the University of Wyoming Science Summer Camp, (Longitude 116° 14′, Latitude 41° 21.5′ N.). Approximately one-quarter of a mile west of the Camp, on a flat-topped ridge, was located the station in which the study was made. A distant view of the vicinity is shown in Figure 1.

VEGETATION

According to Hanna (1934), "the Medicine Bow Mountains form an area which has been and is now favorable to the growth of trees, although there are local areas, in places extensive, like the mountain parks and meadows which for reasons not always clearly apparent, do not support such a covering. Fire has been a very important factor in the determination of the present vegetational types, for the region has been swept thoroughly and repeatedly by severe burns, so that virgin stands of timber occur only in isolated tracts."

FIG. 1. View of the general vicinity of the study from a distance of about 1.5 miles. The approximate location of the station is indicated by the arrow.

The station for this study was in the Snowy Range Natural Area, a declared wilderness tract of 771 acres of broken forest land, recently set aside as a primitive area by the United States Forest Service. It is one of the few timbered areas of the Medicine Bow National Forest that has not been logged since the settlement by white man in southeastern Wyoming, being typical of the Engelmann spruce-subalpine fir association found between 9,000 and 11,000 feet in that region. It lies within the Canadian Life Zone, but very close to the Hudsonian Life Zone, the station being at approximately 10,000 feet altitude.[1]

Though no increment borings were taken, it is interesting to note that stakes cut by Dr. Daubenmire from suppressed individuals of subalpine fir measuring 1 inch D. B. H. exhibited 65 annual rings.

[1] University of Wyoming Summer Camp Bulletin, 33 (5), 1937.

As a part of the subalpine formation, the Engelmann spruce-subalpine fir association is bordered by the montane forest below and the alpine tundra above it. This petran subalpine forest, which reaches its eastern limit on the Front Ranges of the Rocky Mountains from New Mexico northward, "bears a direct relationship to the boreal forest formation, the chief dominants of both belonging to the two genera, Picea and Abies, the species of which are also related" (Weaver and Clements 1929).

Concerning the forest of the immediate locality in which this study was carried on, Daubenmire (communication) states that "only two tree species occur in the mature community: *Picea engelmannii* (Parry) Engelm. (Engelmann spruce), and *Abies lasiocarpa* (Gord.) Parry (subalpine fir). Picea is more conspicuous in the larger size classes, while Abies dominates the smaller, the former attaining the greater size, commonly having a D. B. H. of 60 to 70 cm., whereas the latter seldom exceeds 40 to 50 cm. The forest is dense and closed; the combined basal area of the two trees per 1,000 sq. meters is 7.22 sq. meters."

Hanna (1934) states that in the main spruce-fir forest of the region under consideration, the vegetation consists of few species. *Vaccinium scoparium* Leiberg (bilberry) is the most characteristic ground-cover plant, observed to be growing in the sunnier spots of the forest and forming a discontinuous shrubby cover from 6 to 10 inches high. Two herbs, *Arnica cordifolia* Hook (heart-leaf arnica) and *Pedicularis racemosa* Dougl. (lousewort) compose most of the remaining conspicuous ground-cover, but several sedges, *Carex* spp., occur commonly. Daubenmire, studying in detail the composition of the forest, found, in one hundred 1 sq. meter quadrats over two 1x50 meter transects, that *Vaccinium scoparium* exhibited a frequency of 90%, *Arnica cordifolia* 17%, *Pedicularis racemosa* 11%, and Carex 11%. A low-growing species of Ribes was commonly observed about the bases of large spruce trees.

Figure 2 shows the interior of the station area, especially as regards the low half-shrub form of the *Vaccinium scoparium* in the foreground. In the foreground of Figure 3 is illustrated the nature of the suppressed individuals of subalpine fir that occurred commonly in the area, forming an important part of the undergrowth and varying from 30 cm. to 1 meter in height. At the right of the picture is an Engelmann spruce, at the left, two subalpine firs. The absence of any deciduous undergrowth is to be noted in this view. The down logs in both Figures 2 and 3 are typical of the spruce-fir forest of the Medicine Bow area.

Several species of fleshy fungi were conspicuous in the spruce-fir zone during the latter half of July and early August, principally in the parks and the open spaces of the forest proper. It is possible that the high precipitation in the week of July 6 to 13 may have favored an abnormal abundance. No reference is available concerning the seasonal succession of the fleshy fungi in

this region. It appears evident, however, that the curve of abundance would normally show a high point during the period above noted. In any event the occurrence of these fungi bears directly upon the presence of certain mycetophilous insects.

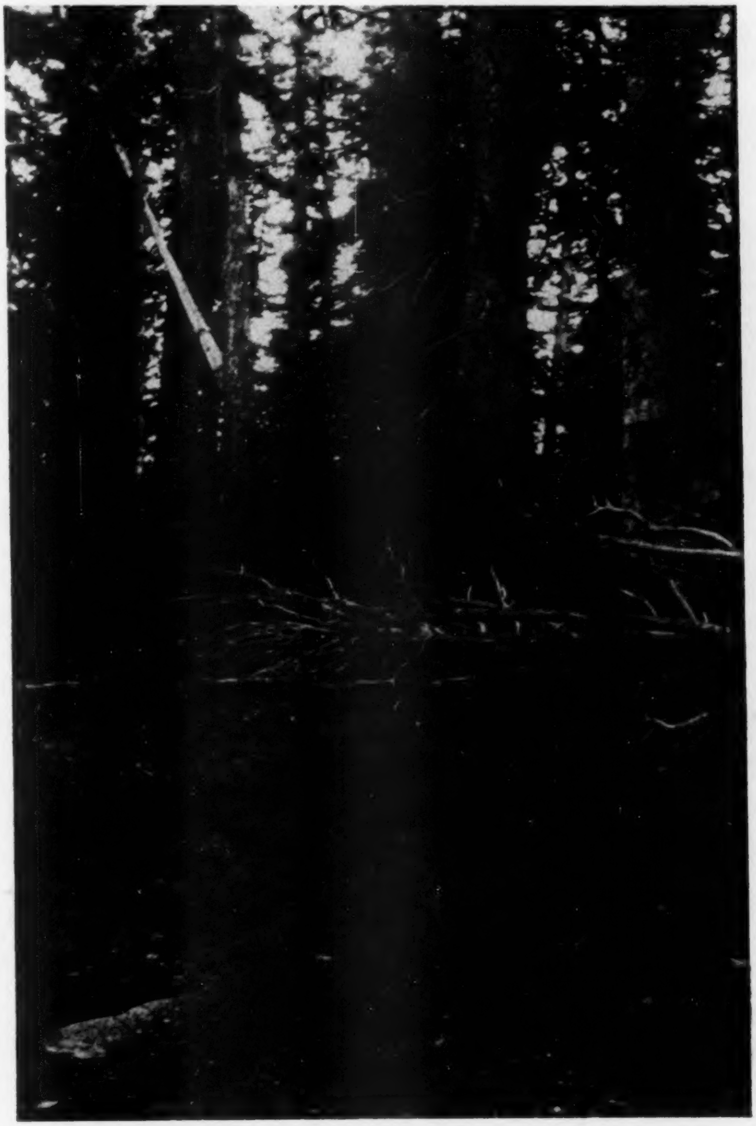


FIG. 2. Interior of the spruce-fir forest studied. The instrument station was located beneath the leaning dead tree in the background.

A noteworthy feature of the spruce-fir zone is the occurrence of natural clearings, known as parks, which interrupt the continuity of the forest. These vary considerably in area, from less than an acre to 10 or more acres, and present a grassland vegetation. Schimper (1903) states that definite prop

erties of the soil may bring forth a character of vegetation that does not belong to the climatic type, and that grassland may occur in many spots where the climate gives rise to forest. These parks appear, then, to be responses to edaphic conditions, their vegetation being determined chiefly by the soil. There is apparently little invasion of the climax trees upon the parks. The lodgepole pine, however, tends to produce in them a scattered population. Figure 4 shows such a park which bordered the writer's station. In the left background can be seen two young Engelmann spruces, and near the center foreground a lodgepole pine which has been distorted following the work of porcupines.

FIG. 3. Interior of the spruce-fir forest studied, showing the nature of the suppressed subalpine fir.

SOIL

The floor of the spruce-fir forest is more or less evenly covered by a relatively thin carpet of litter in the form of conifer needles. Below this appears a layer of duff in which the plant debris has begun to disintegrate. These two layers range from 2-6 inches in thickness, being deepest under heavy cover and shallowest in the open spaces of the forest. Beneath this litter-duff stratum is the mineral soil. A considerable area of the forest floor is covered by fallen logs in all stages of decay. In the last stages these appear as low, rounded mounds, thinly covered by litter and bearing vegetation.

Samples of the duff and soil, and of the highly organic remains of the disintegrated logs were taken for analyses. These data appear in Table 1.

TABLE 1. ANALYSIS OF SOIL AND DUFF SAMPLES FROM SPRUCE-FIR FOREST

Sample 1. Duff, under conifers, supporting only fir reproduction.
Sample 2. Soil beneath sample 1.
Sample 3. Late stage decay, supporting Vaccinium, spruce and fir reproduction, and lichens.
Sample 4. Thin duff layer, open space in forest, supporting Vaccinium, Arnica, fungi, lichens, and a sedge.
Sample 5. Soil beneath sample 4.
Sample 6. Wet, spongy duff, supporting fungi, Arnica, sedge, and fir reproduction.
Sample 7. Soil under sample 6.

Sample	Volatile Matter	Organic Matter	Nitrogen	Hygroscopic Coefficient	pH
1.	65.8	61.7	1.40	41.6	6.3
2.	5.1	2.6	0.08	5.6	4.5
3.	98.1	96.6	0.32	38.5	5.0
4.	49.8	45.2	1.10	29.4	5.4
5.	4.8	2.6	0.80	6.0	4.6
6.	76.7	22.6	1.28	46.8	5.5
7.	27.9	72.3	0.48	22.0	5.5

FIG. 4. View of a park, typical for the spruce-fir zone in southern Wyoming, which bordered on the station area.

Most notable concerning these samples is the consistently high acidity. In three cases samples of soil were taken immediately below samples of duff. In two of these sets the soil shows a markedly lower pH. than the duff above it. This may account for the abundance of certain arthropods in the litter-duff stratum and the comparative absence of any in the soil. A similar condition is described for Maine pine-hemlock forest by Blake (1926).

ENVIRONMENTAL STUDIES AND METEOROLOGICAL INSTRUMENTS

Additional environmental factors investigated were soil temperature, air temperature, relative humidity, wind, light, and evaporation stress. A soil thermograph with the sensitive element buried in the soil at a depth of 0.1 meter below the litter-duff layer, furnished a continuous record of the soil temperature. A hygrothermograph was employed to record the temperature and relative humidity of the air. This instrument was housed in a shelter so placed that the sensitive unit might be at the 0.1-meter level above the forest floor, which height also marked the middle of one of the atmometers.

The recorded curves furnished by the hygrothermograph were translated into weekly mean figures by averaging the hourly air temperatures for day and for night, and the relative humidity values shown at two hour intervals for day and night. Weekly soil temperature means were determined by averaging the hourly temperatures recorded.

Wind velocity was measured with a Robinson type 3-cup anemometer, the cups of which were placed 1 meter above the ground. Readings were made regularly morning and evening: i.e., June 29 to July 29 inclusive, 8 A.M. and 8 P.M.; July 30 to August 24 (A.M.), 8 A.M. and 7 P.M. The record thus determined shows not only the average wind velocity in the forest, but the difference between night and day velocities.

Three Livingston cylindrical porous cup atmometers with non-absorbing mountings were employed to determine comparative evaporation rates, one being placed at each of the three aerial strata studied; i.e., 0.1 meter, 1 meter, and 3 meters, these heights transecting the middle of the respective cups. The reservoir bottle of the lower cup was sunk in the soil, that of the 1-meter cup set in a wooden box which was secured to a root of a fallen tree, and that of the 3-meter cup in a wire basket which was hung from an inclined tree.

The instrument station was located under the leaning dead tree in the left background of Figure 2.

Light intensity was determined with a Weston illuminometer. Readings in foot candles were made at 1-meter intervals along two 20-meter transects on the forest floor. No satisfactory method was worked out for measuring light intensity at various levels along these transects.

The weekly mean average air temperature of the 0.1-meter level shows three high points during the study. These occurred during the weeks ending July 6, July 27, and August 17. These peaks of weekly means do not, however, attain points markedly above the remaining means, showing a maximum range of only 6.2°F. (3.4°C.). The study was begun too late and ended too early to show either the general rise of the spring temperatures or any definite indication of the autumn decline. The wide day-night fluctuations in temperature suggest an accompanying shift in stratal conditions and a possible consequent daily vertical succession in population, pointing to a

need for further and more detailed study of stratal relations. These temperature shifts are somewhat indicated by the range attained by weekly minimum and maximum temperatures, the greatest weekly range of 45.5°F. (25.3°C.) occurring in the week ending July 6, the least, of 20° F. (11.1° C.), in the week ending August 3 (Table 2).

TABLE 2. AIR TEMPERATURE IN DEGREES F. AT 0.1 METER ABOVE THE SURFACE OF THE GROUND

Week Ending	Abs Max	Abs Min	Mean Max	Mean Min	Mean Ave	Max Range	Mean Range	Daily Mean Ave	Nightly Mean Ave
July 6	83.5	38.0	76.0	38.5	53.8	45.5	33.9	60.6	47.0
July 13	73.5	43.0	63.8	46.0	51.8	30.5	17.8	55.9	47.8
July 20	67.0	34.0	59.8	38.3	49.2	33.0	21.5	54.9	43.8
July 27	81.5	42.0	71.0	47.0	55.4	39.5	24.0	61.6	49.3
August 3	66.5	46.5	60.3	47.7	52.6	20.0	12.5	55.8	49.6
August 10	67.0	41.5	57.7	44.7	51.8	25.5	13.0	55.1	48.5
August 17	71.5	44.0	65.0	47.3	53.8	27.5	17.7	59.0	48.6
August 24	72.0	41.0	65.1	47.4	52.7	31.0	17.7	58.0	47.4

A maximum weekly range of 7.0° F. (3.9° C.) and a maximum seasonal range of 8.5° F. (4.6° C.) in the temperature of the soil at 0.1 meter below the litter-duff layer show a marked stability of this factor in this stratum as compared with the ranges of temperature evident in the epiphytic strata studied (Table 3).

TABLE 3. SOIL TEMPERATURE IN DEGREES F. AT 0.1 METER UNDER LITTER-DUFF LAYER

Week Ending	Abs Max	Abs Min	Mean Max	Mean Min	Mean Ave	Total Range	Mean Range
July 6	47.5	41.8	45.7	41.7	44.3	5.7	4.0
July 13	46.0	41.0	43.9	41.6	43.0	5.0	2.3
July 20	47.5	40.5	45.7	43.0	44.5	7.0	2.7
July 27	49.0	44.0	48.0	45.3	46.9	5.0	2.7
August 3	49.0	45.5	47.8	46.0	47.0	3.5	1.6
August 10	48.0	44.0	46.8	45.0	46.0	4.0	1.8
August 17	49.0	46.0	48.1	46.3	47.4	3.0	1.8
August 24	48.0	44.0	47.6	45.5	46.6	4.0	2.0

The relative humidity at the 0.1-meter level, the herb-half-shrub stratum, shows two marked high points and two definite low points, the latter occurring during the first and last weeks of the study, being followed in the first case and preceded in the last by the high points. Neither, however, shows extremes sufficient to be significant in themselves (the greatest being 15.2%), since the fluctuation of a single day showed a maximum value of 66% (Table 4).

TABLE 4. RELATIVE HUMIDITY AT 0.1 METER ABOVE THE SURFACE OF THE GROUND

Week Ending	Abs Max	Abs Min	Mean Max	Mean Min	Mean Ave	Max Range	Mean Range	Daily Mean Ave	Nightly Mean Ave
July 6	77.0	10.5	69.5	20.1	46.3	66.5	49.3	35.0	57.6
July 13	75.0	21.0	71.5	35.7	61.5	54.0	36.0	53.6	69.4
July 20	75.0	19.0	73.7	28.0	57.4	56.0	26.3	47.8	67.0
July 27	83.5	16.5	76.6	28.3	57.1	67.0	48.3	45.1	69.0
August 3	77.0	20.0	73.7	37.6	59.6	57.0	36.1	54.3	64.9
August 10	76.5	19.5	73.0	44.7	60.7	57.0	28.1	54.4	67.1
August 17	86.0	22.0	76.3	39.6	60.8	64.0	36.7	52.5	69.1
August 24	80.0	18.0	71.3	29.6	46.1	62.0	41.7	37.8	54.7

The precipitation record for the vicinity shows a decided and apparently unusual high peak in the week ending July 13. During this period 2.78 inches of rain fell. The nearest approach to this amount occurred in the week ending August 3, but with only .69 inch. Marked low figures appear for the weeks ending July 6 and 27, and August 17 and 24 (Table 5).

TABLE 5. AMOUNT OF RAINFALL* RECORDED BY RAIN GAUGE IN CLEARING

Week Ending	Inches	Total for
July 6	.1	....
July 13	2.78	....
July 20	.56	....
July 27	.29	3.73
August 3	.69	....
August 10	.37	....
August 17	Tr	....
August 24	.04	1.10

* From record obtained at weather station maintained by Dr. G. W. Solheim at the University of Wyoming Science Summer Camp about one-half mile from the instrument station.

Wind velocity, measured at 1 meter above the ground, was very low. The greatest weekly M.P.H. value, .32, is recorded for the week ending August 24 (Table 6).

TABLE 6. WIND VELOCITY AT 1 METER ABOVE FOREST FLOOR, EXPRESSED IN MILEAGE PER WEEK, DAY, NIGHT, AND HOUR

Week Ending	Total Mil	Total Day Mil	Total Night Mil	Ave Day Mil	Ave Night Mil	Max Day Mil	Max Night Mil	Min Day Mil	Min Night Mil	MPH
July 6	38.70	35.75	2.95	5.10	.42	7.60	1.80	3.35	.10	.23
July 13	23.70	19.90	3.80	2.84	.54	4.95	1.35	.80	.15	.14
July 20	22.70	14.80	7.90	2.11	1.12	5.00	2.80	.90	.35	.13
July 27	38.30	31.80	6.50	4.54	.92	8.70	3.25	1.30	.10	.22
Aug. 3	24.20	22.30	1.90	3.18	.27	8.00	.50	1.45	.05	.14
Aug. 10	23.00	16.40	6.60	2.34	.94	4.55	3.60	.70	.40	.13
Aug. 17	44.90	33.00	11.90	4.71	1.70	8.30	6.60	1.20	.10	.26
Aug. 24	55.20	41.20	14.00	5.88	2.00	9.70	4.40	2.70	.90	.32

The weeks ending July 6 and 27 also show comparatively high points in the curve plotted for the season. Had this environmental factor been measured at the 0.1-meter level still lesser values would have been recorded, air movement in this stratum of the forest being reducd to a minimum, due largely to the great number of down logs. Air movement in the forest appears ecologically important to animals only in its relation to evaporation rate, and not through its direct mechanical effect.

"Since the evaporating power of the air has generally come to be considered as the most reliable general index to all other physical factors which affect organisms in terrestrial habitats" (Blake 1926), being a function of the other forces, an attempt was made to measure the comparative stratal values of this factor. The general curve of evaporation shows a decided high point during the week ending July 6, with two lesser peaks occurring during those ending July 27 and August 24. Following each of the first two highs is a marked drop in evaporation, after which the values build up to the succeeding high points (Table 7).

TABLE 7. NUMBER OF CUBIC CENTIMETERS EVAPORATED FROM POROUS CUP ATMOMETERS (Reduced to Standard)

	Height 0.1 meter	Height 1 meter	Height 3 meters
Week Ending:			
July 6	106.43	144.27	181.80
July 13	26.86	38.62	65.30
July 20	33.50	62.76	93.74
July 27	73.00	107.21	144.00
August 3	20.80	34.79	49.24
August 10	25.91	46.93	68.25
August 17	47.08	71.63	100.72
August 24	70.29	95.63	127.94
Total	403.90	601.86	831.02

This picture of evaporation stress shows a correlation with the records of the other factors in this habitat. The three high evaporation values accompany the three high points of air movement, the three low points in precipitation, the lower relative humidity values, and the three temperature peaks. The low evaporation rates accompany lesser wind mileages, increased precipitation, greater humidity values, and decreasing temperatures. The closest correlation appears to be with air movement and relative humidity.

The evaporation curves of the three aerial strata investigated exhibit complete evidence of stratification of this factor in this portion of the forest, the lowest evaporation stress occurring at the 0.1-meter level, the greatest at the 3-meter level, with intermediate values appearing at 1 meter. Weese (1924) found the gradient in the evaporating power of the air in deciduous forest a striking occurrence, strata "less than a meter apart, vertically,

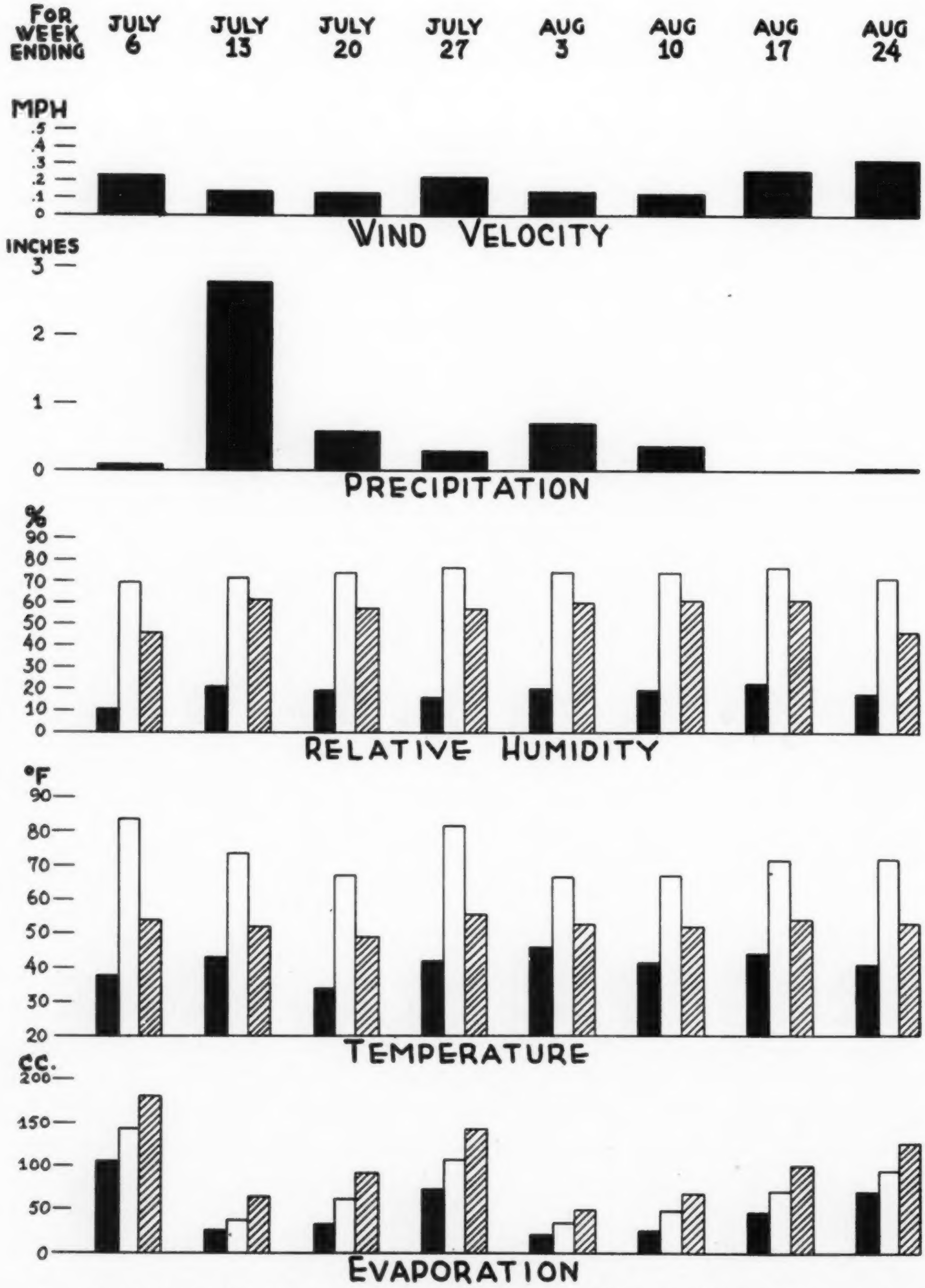


FIG. 5. Meteorological data. In the graphs for relative humidity and temperature the solid bars represent the absolute minimum for each week, the unmarked bars the absolute maximum, and the bars diagonally hatched the weekly mean average. In the graph showing evaporation rates, the solid bars represent the rate per week at 0.1 meter above the forest floor, the unmarked bars the rate at 1 meter height, and the diagonally hatched bars the rate at 3 meters.

showing definite and constant differences," particularly at the lower levels. Blake (1926) has shown this to be equally true for Maine pine-hemlock forest, "and even more regular and constant." The writer's findings in Wyoming spruce-fir forest parallel those of Blake. No intersecting of the evaporation curves for the three strata is shown, and the gradients remain markedly consistent.

According to Livingston (1935) "*vapor-pressure deficit* should replace *relative humidity* in all studies concerned with the *dynamic drying influence* of the environment." Since this study deals especially with stratification, that of environmental factors being determined by atmometers, not by hygrometers, it is considered unnecessary to convert the recorded relative humidity into vapor-pressure deficit.

TABLE 8. LIGHT INTENSITY IN FOOT-CANDLES AT 1-METER INTERVALS ALONG TWO 20-METER TRANSECTS IN SPRUCE-FIR FOREST

TRANSECT No. 1	TRANSECT No. 2	
July 29, 11:55-12:05	August 10, 11:15-11:35	August 10, 11:55-12:05
95	400	1600
1500	2200	280
8900	115	195
2000	190	250
1100	48	270
135	8700	1700
350	250	400
850	145	500
3500	145	160
73	100	100
140	74	520
13	80	1600
79	720	265
110	155	770
69	237	180
50	8100	220
51	290	5200
1700	122	1200
850	297	330
7500	210	1250
Average....1453	1129	849
Mean Average.............	....	1143.2

No study was made of the stratification of light intensities. Light readings at midday along two 20-meter transects on the forest floor showed values ranging from 13 to 8,900 foot candles. The mean average of three such sets of readings is 1,143 foot candles, which is approximately 11% of full sunlight (Table 8). At this altitude of 10,000 feet, however, full sunlight, as measured with an illuminometer, shows an intensity of over 10,000 foot candles. Thus the average intensity on the forest floor is probably slightly less than 11% of full sunlight in this region.

METHODS EMPLOYED IN THE STUDY OF THE ANIMAL POPULATION

The methods of quantitative sampling employed in this study were essentially the same as those used by Weese (1924), Blake (1926), King (1927), Bird (1930), and Beed (1936). A critical review of the quantitative methods that have been used in community studies in animal ecology has been made by Phillips (1931).

The writer feels that the sweep net method of random sampling as practicable in a spruce-fir forest study does not warrant the estimation of areal population of epiphytic societies. The nature of the vegetation, especially at the 1-meter and 2- to 3-meter levels, allowed only scattered strokes with the net. Although care was taken to sweep consistently a uniform volume of vegetation in each stratum, an estimate of the total volume of vegetation per unit area in each stratum would necessarily precede an estimate of the invertebrate population therein. In view of this, the basis employed here for the purpose of comparison of stratal populations is that of unit collection, described below.

Soil and forest floor collections were made with an enclosed quadrat. Only three samples were taken during the eight weeks of the study.

Samplings with a sweep net were made on an average of every fourth day. A unit collection, consisting of ten uniform strokes, each sweeping approximately one meter of vegetation, was made in each of the three aerial strata studied, i.e., the 0-33-cm. level, the 1-meter level, and the 2-3-meter level. This procedure was followed in an effort to arrive at an estimate of the population by unit collection in each of these strata, and hence a comparative estimate of the three stratal populations relative to each other and to time; these data were correlated with certain meteorological information gathered in the same strata.

QUANTITATIVE STUDIES

Since the sweep methods of random sampling as employed in this study do not justify the estimation of areal population of the epiphytic strata, there is no basis for comparing the population of the litter-duff with that of any or all of the strata above ground. The fluctuations of animal numbers within the litter-duff and within the three epiphytic strata studied can, however, be compared. There appears to be little or no correlation between these two population curves for the summer season. The increase in the litter-duff society during the second week was an increase only of the forms resident in that stratum, and a later decrease in their numbers was not accompanied by their increase in any other stratum. Some discrepancy is probably due to insufficient data from the litter-duff layer.

The quantitative results of the sweep collections, on the basis of weekly averages, appear in Table 9, and in the form of a graph in Figure 6.

TABLE 9. ANIMAL POPULATION OF THREE AERIAL STRATA STUDIED, BY STRATA AND AS A WHOLE

Week Ending	Herb Half-shrub Coll	Str Ave	1-meter Coll	Str Ave	2-3-meter Coll	Str Ave	Total
July 6...	3	57	3	38	3	32	127
July 13...	0	—	0	—	0	—	—
July 20...	3	81	3	80	3	52	213
July 27...	2	166	2	51	2	36	253
August 3...	1	57	1	65	1	50	172
August 10...	1	46	1	32	1	37	115
August 17...	2	79	2	32	2	52	163
August 24...	0	—	0	—	0	—	—

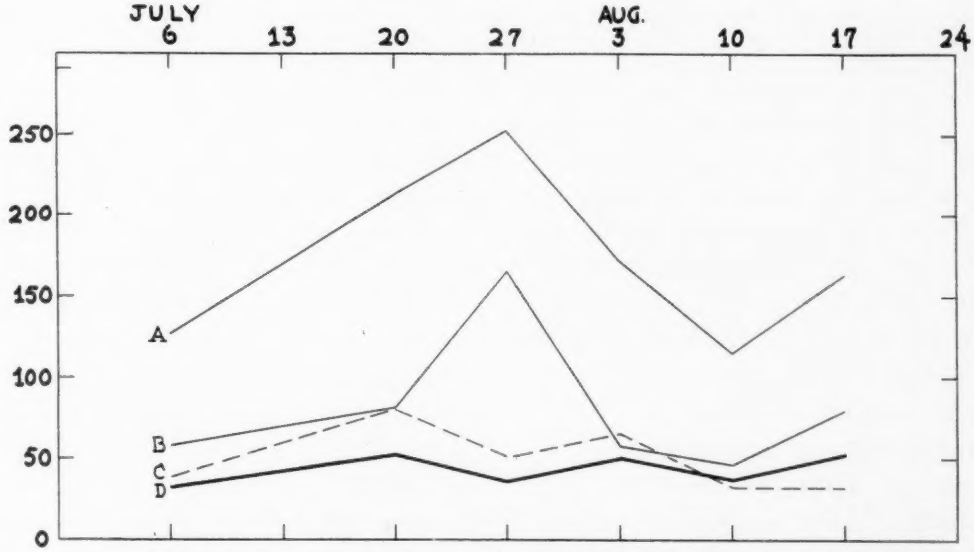


FIG. 6. Biotic Data. Invertebrate animal populations of the three epiphytic strata studied, as a whole and by stratum, based on weekly averages.

A. Total population.
B. Population of herb-half-shrub stratum.
C. Population of undergrowth stratum.
D. Population of low tree stratum.

From a comparatively low aerial population total (Figure 6A) for the week ending July 6, the curve rises uniformly to the high point for the period of study in the week ending July 27. This distinct peak is due to a sudden rise in the herb-half-shrub population which resulted largely from the appearance of enormous numbers of a single genus of ephydrid fly, *Lamproscatella* sp., in the collection of July 20. Following this a steady fall shows the population decreasing to a figure, during the week of August 10, which is slightly below the first low. It then exhibits a definite upward trend for the week following, when the last collections were taken. The curve thus intersects the level of average population approximately at the points representing the weeks ending July 13 and August 3, and again nears that level in the week ending August 17. The central peak of this curve occurs in

a period of mean temperature slightly above any of the other weekly averages, accompanied by a marked peak of high evaporation and low rainfall. It must be remembered, however, that this peak actually received its greatest contribution on July 20, a point in reality between the weeks designated as ending July 20 and 27.

In view of the above, and also of the fact that the mean temperature curve shows too little variation to appear a significant factor, the findings considerably parallel those of Blake (1926) in Maine pine-hemlock forest. He found that marked high points on the curve of total population "appear to be largely due to the presence of certain particular species whose numbers attain a maximum, rather than to any general increase of any considerable number of species making up the population." This remark, in view of the sudden numbers of Lamproscatella, is relevant here. It will be noted that the upward trend at the end of the study is largely due to another increase of this genus of shore fly.

Examining now the size of the three aerial stratal populations (Fig. 6), it is seen that the herb-half-shrub stratum contains the largest, and as a result of the advent of Lamproscatella, the most fluctuating arthropod population. This condition agrees with the findings of Weese for deciduous forest, but is at variance with the condition described for coniferous forest by Blake, where the population of the shrub stratum is almost consistently larger than that of the herb stratum.

The curves given in Figure 6 show that the number of herb-half-shrub arthropods is exceeded by that of the undergrowth stratum forms by a narrow margin during the week ending August 3 only. The herb-half-shrub stratum largely controls the curve of the general aerial population investigated. By maintaining a quantity varying from a low of 10.5% of the total population for this stratum in the week ending August 3, to a high of 48.1% during the week ending August 17, Lamproscatella controls the curve of the herb-half-shrub population.

Attention is now turned to consideration of what appeared to be the prevalent forms of each of the strata. Because of the remoteness of the area studied and the consequent lack of taxonomic knowledge of many of the arthropods collected, only genera can at present be named as prevalents. The inclusion of some specifically determined forms might at first appear as a discrepancy, but in these cases only the one species of the particular genus occurred. Therefore, the basis for determining prevalents and for comparing them, in this instance, remains intact.

A genus, to be accorded the rank of stratal prevalent, must show a numerical preeminence over any other single genus of the stratum. Such preeminence is usually concomitant with a marked degree of stratum choice; this, however, is not always true. A genus may show a population sufficiently large in one stratum to make it the prevalent therein, yet exhibit

greater numbers in another stratum where it ranks below another prevalent. The problem is complicated by the fact that, in response to vertical shifts in physical factors, a genus may exhibit vertical migrations (Shelford 1912b) by which it loses prevalence in one stratum and acquires it in another over some other genus already prevalent there. That the evaporating power of the air at three meters above the ground may be less during one week than that at the 0.1-meter level during another is shown in Figure 5. A genus primarily responsive to this factor of the environment (Shelford 1912a) and normally confined to the latter stratum might for a time exhibit a migration upward and appear as an important constituent of the former.

Figure 7 shows the vertical distribution of the four stratal prevalents in each of the four strata, based on weekly averages and, for convenience in correlation, the curves of evaporation by stratum, and of temperature and rainfall. These biotic data are presented under different organization in Figure 8, which shows in each unit (i.e., A, B, C, and D) the stratal curves of each prevalent animal. A list and discussion of the stratal prevalents of the aestival society follow.

Litter-duff Stratum

Prevalent: *Eremaeus* sp. (Acarina)

Herb-half-shrub Stratum

Prevalent: *Lamproscatella* sp. (Ephydridae; Diptera)

Undergrowth Stratum

Prevalent: *Trichoribates* sp. (Acarina)

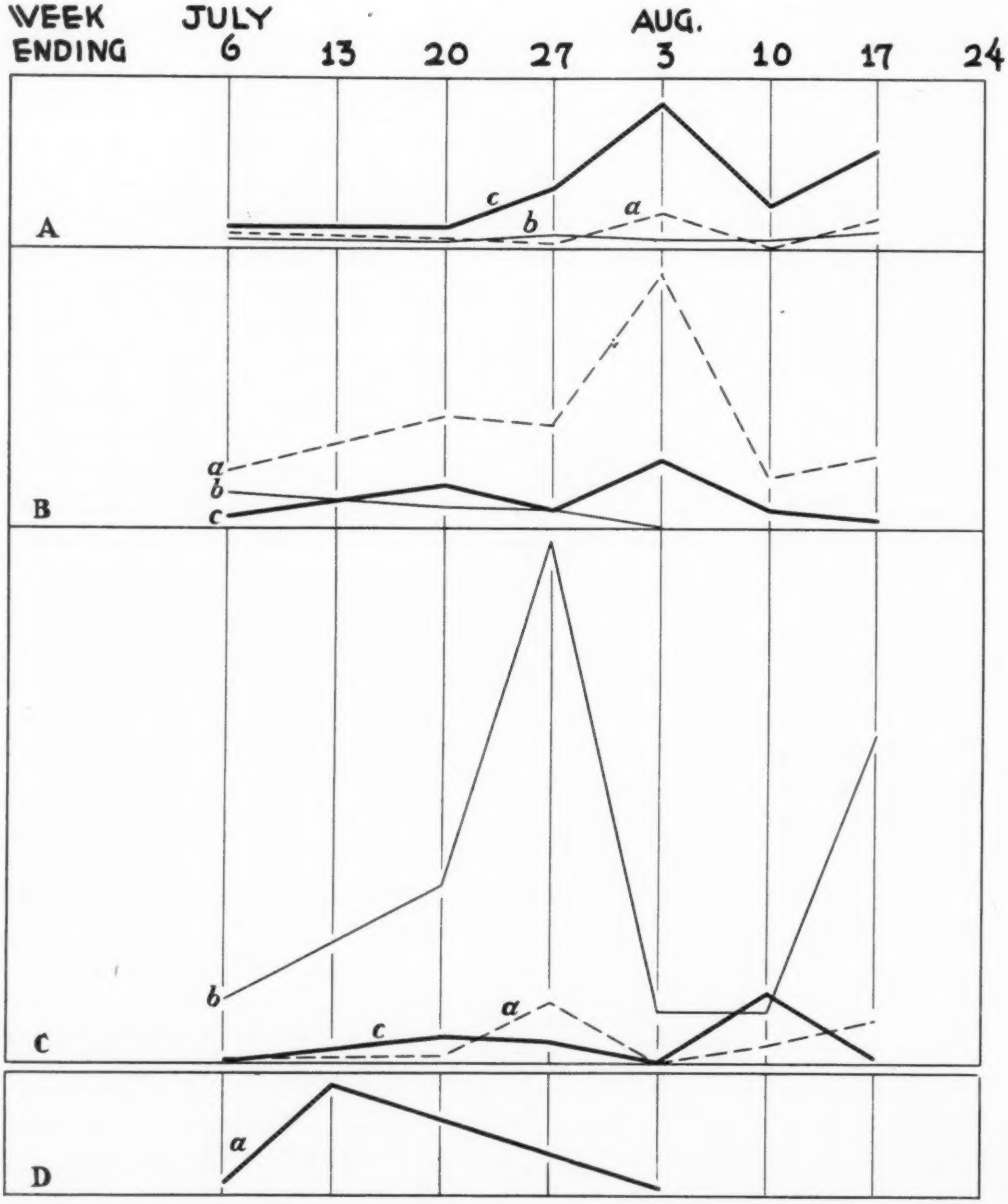
Low Tree Stratum

Prevalent: *Arytaina ribesiae* Crawf. (Homoptera)

LITTER-DUFF STRATUM

Eremaeus sp. Fig. 7, Da; Fig. 8, D

This mite is a permanent resident of the litter-duff stratum, at least during the summer season. It is a saprophytic acarine, and due to its numbers, must possess a considerable importance in its effect upon the decaying organic material of its stratum. The fact that it never appeared in any other stratum during the period of the study shows it to be confined to the litter-duff. The first collection in this layer, in which Eremaeus showed a relatively low abundance, was taken in a partially open spot in the forest, in a thick stand of bilberry *(Vaccinium scoparium)*. The second was under a small spruce tree, and this collection yielded the high number shown in Figure 7. The third, again showing low abundance, was in an opening in the forest. A difference in moisture conditions may have been the causative factor for the differences in numbers, since no vertical migration was apparent. However, Onychiurus (Collembola), common in this stratum,



showed in the third collection an increase in numbers over the second. The peak of abundance for Eremaeus was during the week ending July 13, when the weekly high point of the season's rainfall was also reached. This may or may not have accounted for the maximum abundance. The data are too scanty to be decisive.

HERB-HALF-SHRUB STRATUM

Lamproscatella sp. Fig. 7, Ab, Bb, Cb; Fig. 8, Ca, b, c.

This ephydrid fly showed the greatest numbers of any genus taken. The

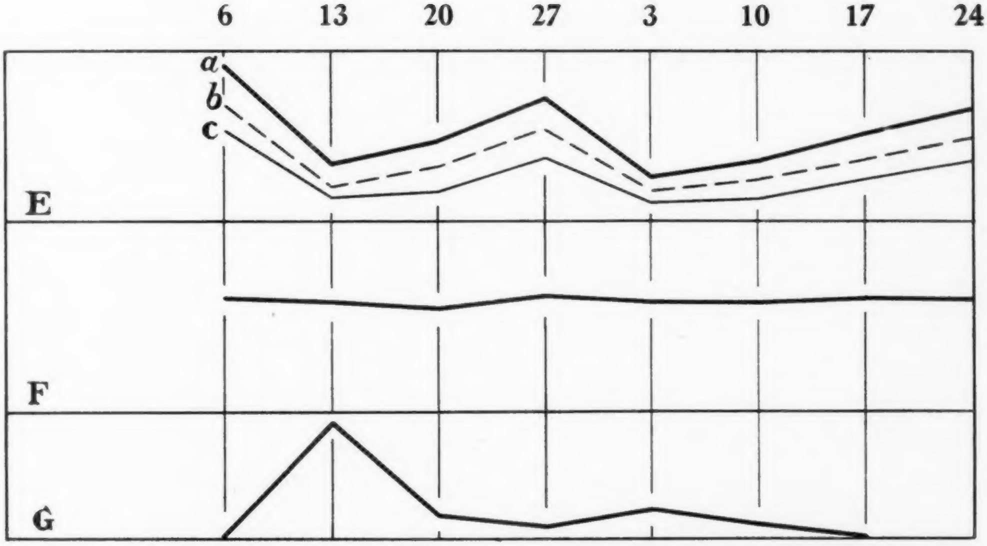
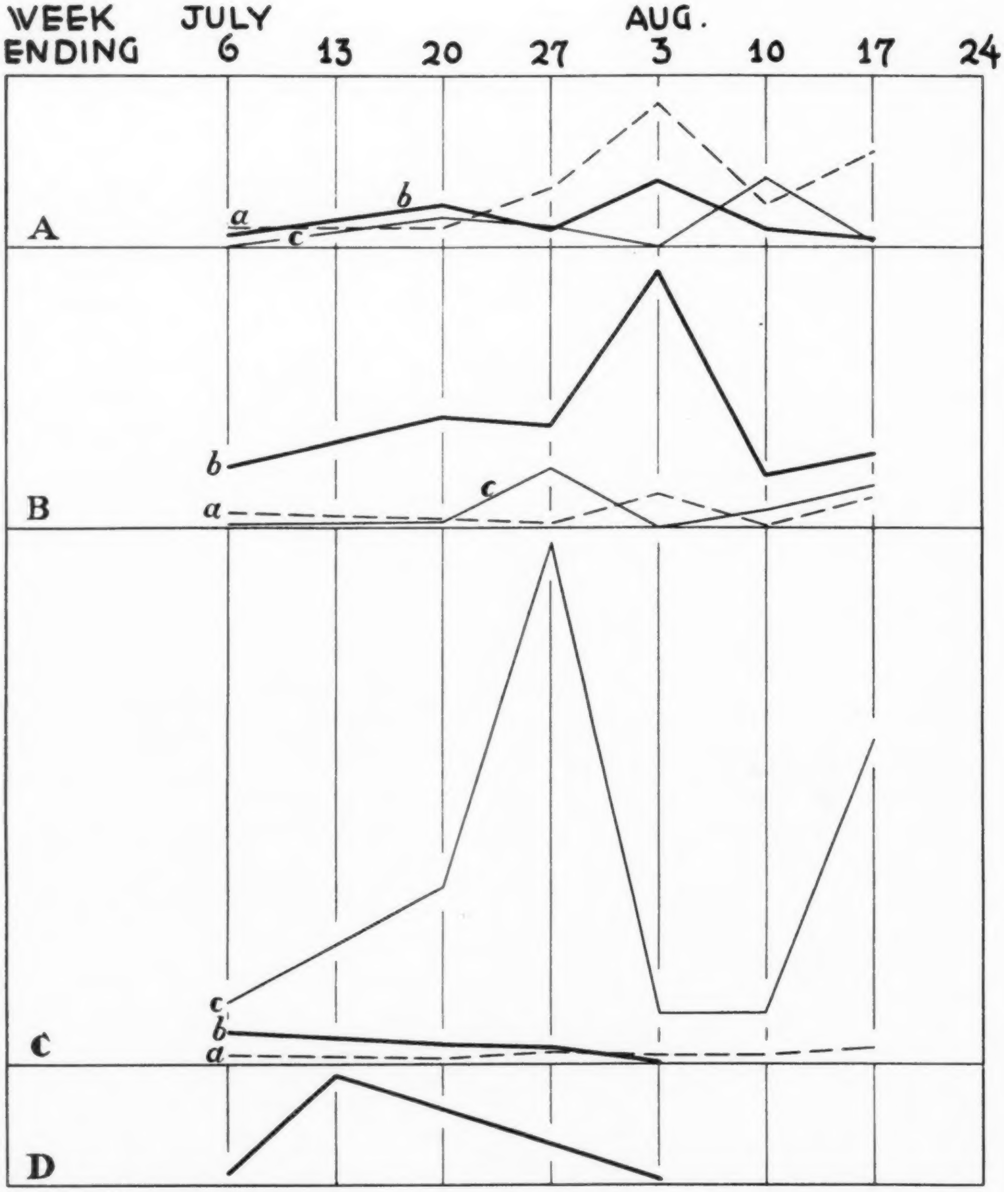


FIG. 7. Biotic data. Stratal distribution of stratal prevalents, based on weekly averages, and correlative climatic data.

A. Low tree stratum.
  a. *Trichoribates* sp.
  b. *Lamproscatella* sp.
  c. *Arytaina ribesiae* Crawf.
B. Undergrowth stratum.
  a. *Trichoribates* sp.
  b. *Lamproscatella* sp.
  c. *Arytaina ribesiae* Crawf.
C. Herb-half-shrub stratum.
  a. *Trichoribates* sp.
  b. *Lamproscatella* sp.
  c. *Arytaina ribesiae* Crawf.
D. Litter-duff stratum.
  a. *Eremaeus* sp.
E. Evaporating power of the air.
  a. In low tree stratum.
  b. In undergrowth stratum
  c. In herb-half-shrub stratum.
F. Temperature in herb-half-shrub stratum, by weekly means.
G. Precipitation.

first peak of abundance on July 20 came during the flowering period of the half-shrub, *Vaccinium scoparium*. It appeared largely confined to the stratum named after the life form of this bilberry. While the peak of its abundance for the week ending July 27 coincides with a high point in evaporation stress, slightly increased mean temperatures, and low rainfall, any significance is largely lost when it is noted, as previously stated, that Lamproscatella presented excessive numbers in only one collection, the curve falling off sharpely four days later. It seems significant, however, that although



showing a greater population than any other form, it exhibited less vertical migration. Lamproscatella, belonging to a family of flies stated to be "found in moist places" (Curran 1934), was largely resident in the herb-half-shrub stratum, probably due to a combination of physical and biotic factors.

UNDERGROWTH STRATUM

Trichoribates sp. Fig. 7, Aa, Ba, Ca; Fig. 8, Ba, b, c.

That a genus of mites known to be saprophytic (Jacot, communication) should appear as the prevalent form of this stratum, while another mite

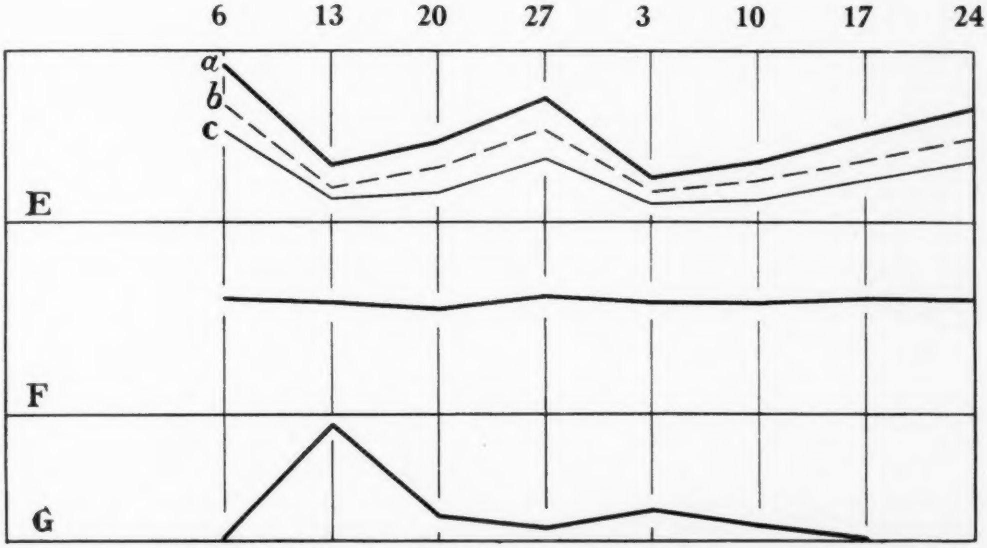


FIG. 8. Biotic data. Stratal distribution of stratal prevalents, based on weekly averages, and correlative climatic data.

A. *Arytaina ribesiae* Crawf.
- a. Population in the low tree stratum.
- b. Population in the undergrowth stratum.
- c. Population in the herb-half-shrub stratum.

B. *Trichoribates* sp.
- a. Population in the low tree stratum.
- b. Population in the undergrowth stratum.
- c. Population in the herb-half-shrub stratum.

C. *Lamproscatella* sp.
- a. Population in the low tree stratum.
- b. Population in the undergrowth stratum.
- c. Population in the herb-half-shrub stratum.

D. *Eremaeus* sp. Litter-duff population.

E. Evaporating power of the air.
- a. In low tree stratum.
- b. In undergrowth stratum.
- c. In herb-half-shrub stratum.

F. Temperature in herb-half-shrub stratum, by weekly means.

G. Precipitation.

(Eremaeus) of similar food habits occurs as the resident prevalent of the litter-duff, is particularly significant. The stratum choice of Trichoribates is distinctly the undergrowth stratum (1 meter). Its prevalence is marked, both in relation to the occurrence of the other stratal prevalents in this stratum (Fig. 7 B), and as regards its own vertical distribution, its numbers in other strata never exceeding those in its chosen stratum (Fig. 8 B). Its numbers at all times during the summer exceeded those of any other genus of the undergrowth stratum.

It will be noted that its population peak occurred in the week ending August 3. During the week preceding, which was distinguished by high evaporation, its numbers in this stratum showed a slight decrease with an increase appearing in the herb-half-shrub stratum. The week of August 3 showed extremely low evaporation rates, and during this period the undergrowth stratum gained abruptly in numbers of Trichoribates. The low tree stratum, heretofore showing very few mites, exhibited a slight increase, and the herb-half-shrub stratum showed a complete absence of this mite. In the following week the entire Trichoribates population fell off, but in the next week, the last of the study, that of all strata was showing a slight upward trend.

Trichoribates evidently offers an example of marked sensitivity to factor shifts which are in this case expressed only by evaporation stress, and with Eremaeus, shows decided stratum preference.

Low Tree Stratum

Arytaina ribesiae Crawf. Fig. 7, Ac, Bc, Cc; Fig. 8, Aa, b, c.

This homopteran presents less stratum choice than the prevalent forms thus far discussed, but possesses sufficient factor sensitiveness to warrant attention. Occurring in numbers large enough to make it conspicuous in the undergrowth stratum, it assumes the prevalent role in the low tree stratum.

The low tree stratum (3 meters) yielded the lowest animal population of any epiphytic stratum investigated (Fig. 6 D). The numbers were extremely low here until during the week ending July 27 when the population of *Arytaina ribesiae* began to increase, producing a high point in the following week. This was accompanied by an increase in its numbers in the undergrowth stratum, and a decrease in the values it had built up in the herb-half-shrub stratum, the shift occurring during a period of low evaporation. This apparent correlation loses significance in view of the data for the following week. Here, during a time when there was only slight increase over the low evaporating power of the air for the preceding week, the low tree and undergrowth populations of *A. ribesiae* decreased sharply, while the herb-half-shrub population increased abruptly to a value above that of its preferred stratum. Furthermore, during the next week, with still slightly increasing rates of evaporation, the undergrowth population continued to decrease, but the low tree numbers showed an increase and the curve for the herb-half-shrub stratum trends downward. Thus it would seem that this homopteran showed a lesser degree of responsiveness to shifts in physical factors than the two genera of mites discussed above, and that, although it maintained its prevalence in the low tree stratum, its prominence therein depended largely upon the absence of other highly numerous forms.

DISCUSSION

The spruce-fir forest is a habitat exhibiting measurable stratal differences in physical factors. These factors probably show a more or less graded vertical series in the forest, the distinction of strata being, of course, an arbitrary one. The strata especially investigated were the herb-half-shrub stratum (0.1 meter), the undergrowth stratum (1 meter), and the low tree stratum (3 meters). The physical differences of these strata were determined by relative measurements of the evaporating power of the air. Since this force has been shown to be a "fairly reliable index to other physical factors" (Blake 1926), it is assumed that stratification in the coniferous forest studied is also expressed by gradients of temperature and humidity.

If temperature data for the soil are any indication of the range of that factor in the litter-duff, this latter stratum presents an environment of comparatively low but markedly uniform temperatures. This is somewhat reflected by the apparent confinement of adult arthropod forms to this stratum during the summer season.

A steeper gradient probably exists between the litter-duff stratum and the herb-half-shrub stratum, than between any two of the epiphytic strata investigated. This study disclosed an especially marked difference in the range of temperature fluctuation in these two environments, the herb-half-shrub showing wide daily and weekly ranges. As regards this factor, the inhabitants of all epiphytic strata at this altitude experience serious daily shifts, and more investigation is needed to show their responses.

Due to the nature of the spruce-fir reproduction and to the abundance of prostrate logs, the air movement, already at very low velocity in the forest, is reduced to practically nil in the herb-half-shrub stratum. This means a minimum of evaporation stress and a consequent environment of comparatively moist air. Prevailing groups here were dipterans, forming the bulk of a population whose average exceeded that of any other stratum. Showing decided stratum preference, both the prevalent and the less numerous genera of flies were apparently responsive to physical factor shifts. The probable complicating factor of emergence calls for further study.

The prevalence in the undergrowth stratum of a genus of mites, the food habits of which are similar to a different mite found in the litter-duff points to an apparent stratum preference chiefly on the basis of physical factors.

The evaporating power of the air in the undergrowth stratum maintained a constant level above that of the herb-half-shrub environment; the same was true to approximately the same degree of the low tree stratum over the undergrowth. Since, however, the distance between the instruments representing the two latter strata was twice that separating the first two, it is evident that the gradient in physical factors, indicated here by evaporation stress, decreases upward. This was shown to be true in Maine

pine-hemlock forest by Blake (1926). The animals found in the two upper strata of the spruce-fir forest in general showed wider vertical distribution than those of the herb-half-shrub stratum. This is indicative either of less marked stratum preference, or of a biotic accompaniment of decreasing gradients in physical forces.

The arthropod population, studied to a height of 3 meters, shows recognizable divisions into stratal societies (layer societies of Shelford 1932), characterized by the prevalent forms. The picture of stratal distribution is complicated by shifts in physical factors which tend to telescope or extend vertically the environmental limits of the vertically distributed arthropod population of the forest. The consequent phenomenon of vertical migrations from layer to layer makes the stratal groupings subordinate in the biota (Shelford 1932). These indications of stratum preference, and of shifting stratum preference, ascribe to prevalent species possible *indicator values* as regards the forces of the layer wherein they are at any given time flourishing. Such values will in the final analysis, however, depend upon the environmental requirements of the individual species. This condition may suggest fruitful investigational approaches to the problem of thorough ecological measurement of a biota.

Evidence is not yet sufficient to indicate the relative values of biotic and physical factors, although, as expressed by Blake (1926), both are determining forces.

Considering the curves of the epiphytic stratal prevalents, it is seen that the peaks of maximum abundance occur from the week ending July 20 through the week ending August 3. Following this is shown a general decrease, which is succeeded by another increase. The decrease falls within a period of general low evaporation stress, and may be a result of this condition, many of the forms having migrated vertically to points above the level of collection. These curves may indicate an aestival maximum, with the last upward trend being evidence of the increase toward an autumnal maximum, similar to that found by Blake in Maine pine-hemlock forest.

It is evident that the data are too insufficient to support anything but tentative conclusions. The complex of factors and the interrelations of biotic forms in the spruce-fir forest call for further study.

SUMMARY AND CONCLUSIONS

1. The Wyoming spruce-fir forest habitat, studied in summer at an elevation of 10,000 feet, shows a measurable stratification of physical environmental factors, determined in this study for evaporating power of the air only. Evaporation stress increases with elevation above the forest floor, as shown by comparative evaporation rates from atmometers exposed at 0.1 meter, 1 meter, and 3 meters.

2. Considering the rate of evaporation at the 3-meter level as 100%, the rates at the 0.1-meter level and the 1-meter level were 48.6% and 72.4%, respectively.

3. Stratification of physical factors of the environment, governed by the dominant forest cover (Shelford 1912a), results in a stratification of the arthropod biota as determined by random sweep collections in the vegetation at these levels, and expressed by the composition and distribution of animal stratal societies. Such groupings are not permanent, even during the summer season. They show vertical shifts in position and changes in composition in response to vertical shifts in physical factors. They are therefore subordinate.

4. Consecutive weekly evaporation rates exhibited differences as great as 74.6%; relative humidity records show a maximum range within a week as great as 67.0%, a mean range of 49.3%, and a maximum range of 74.5% for the season; temperature showed maximum range values as great as 45.5° F. (25.3° C.) within a single week with a mean range value of 33.9° F. (17.7° C.), and a maximum seasonal range of 49.5° F. (27.5° C.). These data, collected during July and August, provide evidence that pronounced shifts in physical factors do occur in the lower epiphytic strata of the spruce-fir forest at 10,000 feet.

Such marked ranges in temperature did not occur in the litter-duff stratum.

5. A prevalent of any stratal society gaining its prevalence through response to physical factors, in part at least, is therefore probably of value as an indicator of immediate environmental conditions.

6. Saprophytic acarines appeared as the prevalent of the litter-duff and the undergrowth strata. Diptera prevailed in the herb-half-shrub stratum, while a homopteran was the prevalent in the low tree stratum.

7. Although biotic factors of the environment undoubtedly exert considerable influence in producing stratification of animal societies, they were not investigated in this study.

8. Complicating the picture of stratal animal societies is the occurrence of seasonal societies, somewhat indicated in the study by the appearance of an aestival high point in total population and in the numbers of prevalent forms, and of an upward trend at the close of the study, suggesting a possible autumnal peak.

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APPENDIX

TABLE 10. LIST OF ARTHROPODS TAKEN IN SPRUCE-FIR FOREST; JUNE 29-AUGUST 24, 1936

The strata in which the following species were collected are indicated in the following manner: HHS, herb-half-shrub; LD, litter-duff; LT, low tree; S, soil; U, undergrowth.

Arachnida
- Araneida
  - Linyphiidae
    - *Bathyphantes formica* Emerton (U)
    - *Ceraticelus crosbyi* Bryant (HHS, LT)
    - *Lepthyphantes* sp. (LD, HHS, U, LT)
    - *Linyphia phrygiana* C. Kock (U, LT)
    - *Linyphia* sp. (HHS, U, LT)
    - *Microneta* sp. (LD)
    - *Tmeticus* sp. (S, LD)
  - Argiopidae
    - *Araneus displicata* (Hentz) (LT)
    - *Araneus* sp. (HHS, U, LT)
  - Dictynidae
    - *Dictyna* sp. (U, LT)
  - Lycosidae
    - *Pardosa* sp. (On forest floor)
  - Thomisidae
    - *Philidromus* sp. (LT)
- Acarina
  - Oribatidae
    - *Eremaeus* sp. (LD)
    - *Nothrus* sp. (U)
  - Bdellidae
    - *Bdella oblonga* (LD)
  - Erythraeidae
    - *Erythraeus* sp. (HHS, U, LT)
    - *Anystis* sp. (HHS, U, LT)
  - Tetranychidae
    - *Bryobia pratensis* (HHS, U)
    - *Liacarus* sp. (LD)
    - *Zercon* sp. (LD)
    - *Techtoribates* sp. (LD, HHS)
    - *Pelops* sp. (LD)
    - *Trichoribates* sp. (LD, HHS, U, LT)
    - *Eupodini* sp. (LD)
    - *Biscirus* sp. (HHS)
    - *Ceratozetes* sp. (HHS, U, LT)
    - *Liebstadia* sp. (LT)

Insecta
- Collembola
  - Entomobryidae
    - *Entomobrya* (near *griseo-olivata* Packard) (HHS)
    - *Entomobrya multifasciata* Tullberg (HHS)
    - *Entomobrya* sp. (U, LT)
    - *Isotoma olivacea* Tullberg (LD)
    - *Isotoma viridis* Bourlet (S, LD)
  - Poduridae
    - *Onychiurus ramosus* Folsom (LD)
  - Sminthuridae
    - *Sminthurus* sp. (HHS, U)
- Corrodentia
  - Psocidae
    - *Caecilius perplexus* Chapman (U, LT)
    - *Liposcelis niger* Bks. (LD)
- Plecoptera
  - Nemouridae
    - *Nemoura* sp. (LT)
- Homoptera
  - Chermidae (Psyllidae)
    - *Aphalara calthae* L. (HHS, LT)
    - *Aphalara pulchella* Crawf. (LT)
    - *Arytaina ribesiae* Crawf. (LD, HHS, U, LT)
    - *Psyllia americana* var. *flava* Crawf. (HHS, U, LT)
    - *Trioza frontalis* Crawf. (HHS, U, LT)
    - *Trioza nigrilla* Crawf. (U)
    - *Balclutha punctatus* (Thunb)
- Hemiptera
  - Miridae
    - *Deraeocoris piceicola* Kngt. (U, LT)
    - *Dichrooscytus* sp. (U, LT)
    - *Dicyphus agilis* Uhl. (HHS)
  - Anthocoridae
    - *Anthocoris* sp. (LT)

Lygeidae
Lygus approximatus Stal. (U, LT)
Nabidae
Nabis alternatus Parshley (HHS)
Trichoptera
Limnophilidae
Limnophilus sp. (U)
Sericostomatidae
Genus undescribed (LT)
Lepidoptera (Larvae and pupae)
Noctuidae, spp. of (HHS, U)
Autographa sp. (LT)
Blastobasidae (LD)
Geometridae (HHS, U, LT)
Nymphalidae (HHS)
Olethreutidae (U)
Coleoptera
Staphylinidae
Atheta sp. (LD)
Cantharidae
Cantharis sp. (LD)
Podabrus sp. (HHS)
Melyridae
Genus and species probably new (HHS, LT)
Scarabaeidae
Aegialia terminalis Brown (LD)
Chrysomelidae
Syneta carinata Mann (U, LT)
Phyllotreta pusilla Horn (HHS, U, LT)
Cryptophagidae
Cryptophagus sp. (LD)
Curculionidae
Magdalis gentilis Lec. var. ? (LT)
Melandryidae (U)
Colydiidae (LD)
Diptera
Simuliidae
Prosimulium sp. (U, LT)
Chironomidae (HHS, U, LT)
Imm. (LD)
Ceratopogonidae (HHS, U, LT)
Psychodidae
Psychoda sp. (U)
Culicidae
Aedes sp. (HHS, U, LT)
Aedes punctor (Kirby) (LT)
Cecidomyiidae
Colpodia sp. (LD, HHS)
Contarinia sp. (HHS)
Monardia sp. (HHS)
Prionellus sp. (HHS)
Trifili sp. (HHS)
Imm. (LD)
Sciaridae
Sciara acuta (HHS)
Sciara diluta (HHS)
Sciara impatiens (HHS)
Sciara karilis (U)
Sciara longispina (HHS, U)
Sciara munda (HHS)
Sciara nigricans (HHS)
Sciara paralis (HHS)
Sciara prolifica (HHS)
Sciara varians (HHS)
Imm. (LD)
Mycetophilidae
Boletina sp. (HHS, U, LT)
Boletina sciarina var. (HHS, U)
Boletina sobria (HHS)
Cordyla recens (LT)
Mycetophila sp. (HHS)
Polylepta sp. (U)
Sceptonia nigra (HHS)
Zygomia ornata (HHS)
Zygomia sp. (HHS)
Imm. (LD)
Bibionidae
Bibio sp. (HHS, LT)
Empidae
Rhamphomyia sp. (HHS)
Bicellaria longipes Loew.
Dolichopidae
Campsicnemus claudicans Loew. (HHS, LT)
Hydrophorus sodalis Wheeler (U)
Phoridae (HHS, U, LT)
Imm. (S)
Trupaneidae
Tephritis acutangula Thom. (LT)
Tephritis araneosa Coq. (U)
Tephritis clathrata Loew. (HHS, U, LT)
Chloropidae
Oscinella sp. (HHS)
Ephydridae
Lamproscatella sp. (HHS, U, LT)
Paralimna sp. (HHS, LT)
Psilephydra sp. (LT)
Philygria debilis Lw. (HHS, U, LT)
Ephydra sp. (U)
Parydra sp. (HHS)
Scatella sp. (HHS)
Scatophila sp. (HHS)

Agromizidae
- *Phytomyza* sp. (HHS, U, LT)
- *Phytomyza praecox* Meig. (U)

Muscidae
- *Hylemya* sp. (HHS, U, LT)
- *Parallelomma* sp. (HHS, U)
- *Hydrotaea dentipes* Fabr. (U, LT)
- *Helina* sp. (LT)
- *Cordylura* sp. (HHS)
- *Hexamitocera vittata* Coq. (LT)

Helomyzidae (U)

Otitidae
- Imm. (LD)

Scatophagidae
- *Scatophaga* sp. (HHS, U, LT)
- Imm. (LD)

Simuliidae

Anthomyiidae (U)
- Imm. (LD)

Rhagionidae
- Imm. (LD)

Epidosidae

Diplosidae

Hymenoptera

Ichneumonidae
- *Phaeogenus* sp. (HSS)
- *Hemiteles* sp. (HHS, U, LT)
- *Bathymetes* sp. (HHS)
- *Atractodes* sp. (HHS)
- *Dialipsis* sp. (U, LT)
- *Polyblastus* sp. (LT)
- *Orthocentrus* sp. (LT)
- *Hyposoter* sp. (U)
- *Angitis* sp. (LT)

Braconidae
- *Rogas* sp. (U, LT)
- *Apanteles* sp. (U)
- *Phaenocarpa* sp. (HHS)
- *Rhysipolis* sp. (LT)

Diapriidae (Serphoidea)
- *Xenotoma* sp. (HHS, U)
- *Belyta* sp. (HHS)
- *Anaclista* sp. (HHS)
- *Paraclista* sp. (HHS)

Tetrastichidae
- *Tetrastichus* sp. (HHS)

SOME FEATURES OF THE VEGETATION OF THE COLUMBIA RIVER GORGE WITH SPECIAL REFERENCE TO ASYMMETRY IN FOREST TREES[1]

By

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University of Minnesota

[1] Botanical contribution from the Johns Hopkins University, no. 146.

CONTENTS

SOME FEATURES OF THE VEGETATION OF THE COLUMBIA RIVER GORGE WITH SPECIAL REFERENCE TO ASYMMETRY IN FOREST TREES

PREFACE

The earliest authentic information concerning the Gorge of the Columbia River was supplied by members of the famous Lewis and Clark Expedition, which passed through it on the last lap of the overland journey to the Pacific in October, 1805, and returned through it in April, 1806 (Thwaites, 1904-1905). Among earlier explorers, Lieutenant William Robert Broughton, of the Vancouver Expedition, had been the only one to ascend the river far enough to see the western portal of the gorge, which he had done in the fall of 1792 (Barry, 1932; Vancouver, 1901); but he did not enter the gorge itself. The first navigator to recognize the mouth of the Columbia was a Spaniard, Bruno Heceta, who had reached that region of the coast in the late summer of 1775; he had been unable to enter the river because of swift currents. Later navigators had seen the river mouth but its fearful bar had turned them away, and it was not until May 11, 1792, that Captain Robert Gray, of Boston, had successfully crossed the very difficult bar and named the great river in honor of his good ship "Columbia"; he seems to have been satisfied with this accomplishment, however, for he turned back to the ocean after having sailed upstream no more than a score of miles.

As the reports of Gray and Broughton, and especially those of Lewis and Clark became known, important posts of the fur trade were soon established on the Columbia, first near its mouth, at Astoria, and somewhat later about a hundred miles upstream, at Vancouver, which is within sight of the western portal of the gorge. Then the river rapidly became the main highway for the fur trade of the Northwest, which it was for many years. Subsequently emigrants from the East reached the rich agricultural regions west of the Cascade Mountains via the Columbia, which carried down through its gorge hundreds of rafts laden with settlers and their prairie-schooner wagons. In the first period of rapid agricultural and mining expansion in this region—roughly from 1850 to 1870—steamboats were the main means of transportation, for there was still no overland route through the gorge. Then a wagon road was built on the south bank, but it was little used because of its steep hills and sharp curves. That road was finally abandoned in 1883, with the completion of the first railroad through the gorge, which appropriated parts of its right of way. In 1908 a railroad was completed along the north bank, and in 1915 the Columbia River Highway was opened on the south side of the gorge. More recent developments in this region have included the completion of the Evergreen Highway on the north side, the construction of two interstate bridges to con-

nect the two highways, and the establishment of a transcontinental aviation route through the gorge. In addition to these modern conveniences for rapid transportation, a network of trails on the gorge walls has recently been built by the United States Forest Service and the United States Civilian Conservation Corps; thus the whole gorge is now rather easily accessible. Embracing, as it does, a very broad range of climate, topography, and soils, and showing remarkable evidences of topographic and vegetational history, the gorge offers an inviting field for ecological studies of many kinds. In this paper are reported some results of such studies, which were carried out in the years 1933 to 1937. Funds and general equipment for four seasons of study in the field were made available by my parents, Mr. and Mrs. William C. Lawrence, of Portland, Oregon, and a number of ecological instruments were supplied by Professor Burton E. Livingston, of the Johns Hopkins University. My early interest in the Columbia Gorge was largely aroused through conversations with Professor William Mansell Wilder and Mr. John B. Yeon, both of Portland. Professor Burton E. Livingston and the late Professor Duncan S. Johnson, both of the Johns Hopkins University, have given many helpful suggestions and criticisms while the preparation of this paper was in progress; Dr. W. G. Lynn also of the Johns Hopkins University helped with the field work in the summer of 1933. My wife, Mrs. Elizabeth Gay Lawrence, has been a constant source of aid and encouragement.

PHYSICAL FEATURES OF THE COLUMBIA GORGE

WATER LEVELS AND RIVER GRADIENTS*

The Gorge of the Columbia River lies directly athwart the high barrier of the Cascade Mountain Range, joining the relatively low Columbia Basin on the east with the somewhat lower Willamette Valley on the west. The gradient of the river is remarkably gradual throughout its 55 miles within the gorge, except for a single 7-mile stretch—the Cascade Rapids—extending from Cascade Locks to Beacon Rock. (See Fig. 1.) Within that stretch the "adopted plane of low water" shows a fall from 41.4 feet to 5.8 feet above mean sea-level. At the foot of the rapids ocean tides of a foot or less are to be observed in times of low water; and in the gorge below the rapids the adopted plane just mentioned has a gradient of 0.125 feet per mile. The gradient becomes 0.250 feet per mile at very high flood stage. Above the rapids the gradient of the adopted plane is somewhat less and the full-flood gradient is somewhat greater, being 0.082 feet and 0.292 feet per mile, respectively. At the eastern portal of the gorge the level of the adopted plane is only 44.4 feet above mean sea-level.

Throughout the gorge the main river bed lies from 15 to 75 feet below the adopted level of low water; computed from deepest soundings (see Map

* Note: Since this paper was written water levels have been altered in some respects by the completion of the Bonneville Dam.

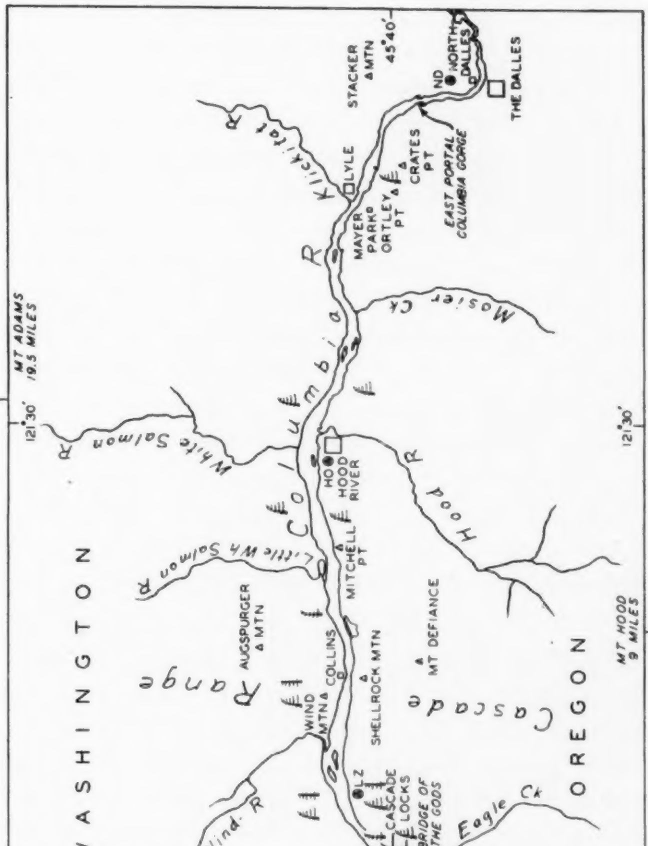

FIG. 1. Outline map of the Columbia River Gorge region. After U. S. Geological Survey (see Map Citation No. 2)

Citation No. 3) at mile intervals, the average depth of the bed below that level is 41.7 feet. For a stretch of several miles above the mouth of Wind River the channel bed is about 30 feet *below* mean sea-level and it is as much as 50 feet below mean sea-level near the west portal.

The nature of the gorge floor, and consequently the characteristics of the floor vegetation, are largely conditioned by very great and fairly regular seasonal changes of water level in the river. According to 55 years of record (1879-1933) at the upper pool at Cascade Locks, which marks the head of the rapids, an annual flood has usually occurred in June, less often in May. The highest stage recorded (June, 1894) is 92.9 feet above sea-level. On the other hand, the river has always been low in winter throughout this period of record, the lowest readings being shown for December, January, or February. The lowest recorded stage (February, 1929) is 38.9 feet above mean sea-level. The average elevation of low water at this pool in winter is 42.8 feet and that of high water in summer is 71.2 feet; thus, the average annual range of fluctuation amounts to 28.4 feet. The greatest annual fluctuation on record is 47 feet (1894) and the least is 14 feet (1926).

The Bonneville Dam, now being built under the auspices of the United States Public Works Administration, about 3 miles below the head of the Cascade Rapids, is planned to maintain at Cascade Locks a mean water level 73 feet above mean sea-level, the minimum being 72 feet, while a level of 92.9 feet would be maintained with all gates open even with a flood as great as that of 1894. Information concerning these levels and the above-mentioned gradients was kindly furnished by Mr. A. L. Darr and Mr. L. F. Henshaw, of the Bonneville Dam Project; part of this information has recently been published (U. S. War Dept., 1936).

Aside from its fluctuation with rise and fall of water level, the width of the water surface of the river naturally varies greatly from place to place according to the conformation of the gorge floor and walls. Its average width throughout the whole gorge is about 0.6 mile, at medium-high water. In its narrowest stretches, near Lyle and in the upper portion of the Cascade Rapids, a width of about 225 yards is maintained whether the river stage is high or low. A corresponding estimate of the river's greatest width—near Multnomah Falls, about eight miles above the west portal—is 1.3 miles at medium-high water.

The soils of the gorge flood plain, as well as its topography, have naturally resulted from river erosion and deposition, and great changes in these may occur in very short periods. Pronounced shifts in the channel and great alterations in channel depth result from every freshet. No long-continued records of erosion or deposition in the gorge are available, but reports indicate that the flood-lands below the rapids have in several instances received from the river in a single season alluvial deposits as much as two or three feet in depth.

THE GORGE WALLS

The walls of the gorge, which represent the truncated ends of the mountain ridges across which the river has cut its way, are in some places very steep while in other places they slope more gently toward the rim. They are broken by large and small lateral canyons, through which tributary mountain streams deliver to the Columbia. At the west portal of the gorge the rims rise to about a thousand feet above the river, and at the east portal their height is about twice as great. In the middle of the gorge, where it intersects the axis of the Cascade Range, the mountains rise to heights of from 3,000 to 5,000 feet. The west portal may be said to lie about 20 miles upstream from Portland (see Fig. 1); but it should be noted that the Oregon wall is continued west for about 5 miles beyond Crown Point, to the mouth of the Sandy River. The east portal is about 5 miles below the city of The Dalles (Fig. 1), but the north wall extends east beyond Stacker Mountain for many miles without significant interruption. The geographic middle of the gorge lies near Wind Mountain, about 8 miles above the town of Cascade Locks. Its walls are highest about two miles east of that point, where Augsburger Mountain, on the north, has an elevation of 3,684 feet and Mt. Defiance, on the south, reaches an elevation of 4,960 feet.

Within 40 miles of the middle three perpetually snow-capped and glacier-laden volcanic peaks—Mt. St. Helens, Mt. Hood, and Mt. Adams (Fig. 1)—rise to elevations of 9,671, 11,225, and 12,307 feet, respectively. Mt. Hood is but 22 miles south of the river and Mt. Adams is 33 miles north of the river. From these two peaks broad valleys lead downward to the gorge, facilitating air drainage as well as water flow. But, although Mt. St. Helens is only 37 miles northwest of the Cascade Rapids it is so cut off from the gorge by ridges and canyons that it can have but little direct influence on gorge conditions.

A general idea of the width of the george, which naturally varies greatly, may be obtained by averaging measurements read from a topographic map (see Map Citation No. 2) at 2-mile intervals throughout the entire length, first for an elevation of 100 feet and then for an elevation of 500 feet above mean sea-level. Thus derived, the average width of the gorge between opposite 100-foot contours is almost a mile, its narrowest width being about 530 yards—near the head of the Cascade Rapids and at Lyle—while its greatest width is about a mile and a half near Stevenson. For the 500-foot elevation, the average width is 1.7 miles and the narrowest width is about a mile—at a number of places above the rapids—while the greatest width is almost 6 miles—at the mouths of the Hood River and the White Salmon River. Between the rims the average width is about 5 miles. In general the Oregon wall of the gorge rises much more steeply than does the Washington wall, and the general elevation of the uplands adjacent to the rims is considerably greater on the Oregon side than on the Washington side.

The rims of the gorge are naturally not continuous, being broken into points and promontories by valleys of various depths and widths. They are deeply broken where the valley of the Hood River and that of the White Salmon River join the gorge from south and north. The valleys of Wind River, Mosier Creek, and Klickitat River also constitute pronounced interruptions where they open into the gorge. The map (see Map Citation No. 2) shows 63 streams entering the Columbia within the limits of the gorge, 31 from the south and 32 from the north. Their west-east distribution reflects the gradation of moisture conditions from the humid western end to the arid eastern end; 41 streams flow into the river west of Wind Mountain and only 22 enter it east of that point. Although an area of about 260,000 square miles of country is drained by the Columbia, only about one per cent of that area is drained by tributaries that enter the river between the two gorge portals. About 77 per cent of the gorge watershed lies on the Washington side while only about 23 per cent is on the Oregon side.

There are many waterfalls in side canyons and ravines, the majority of the spectacular ones occurring on the Oregon wall. They vary from mere rapids to sheer falls of 540 feet (Multnomah Falls). In some the stream descends vertically without wetting its more or less undercut cliff; in others the water cascades down a steep convex cliff, maintaining contact with the rock all the way from top to bottom. As a result of these differences and of differences in the type of basin into which the water tumbles there is much variation in the areas of cliff kept moist by spray.

ROCK FORMATIONS

The main bed rocks of the gorge (Williams, 1916) are worthy of cursory attention, especially because they have naturally played an important role in determining topography and soils. In the middle region of the gorge, where it cuts through the great uplift of the Cascade Mountains, may be seen a large variety of rock types. The lowest and oldest of these is the Eagle Creek formation, with an agglomerate and a conglomerate phase; the former is a volcanic tuff containing numerous angular blocks of andesitic lava, and the latter consists of well-rounded andesitic boulders and pebbles imbedded in sandy matrix. At many places fossils of Ginkgo and contemporaneous species are enclosed in shaly seams, and this formation has consequently been assigned to the upper Oligocene or lower Miocene (Chaney, 1920, 1927). Being rapidly eroded by running water, it has given rise to but few waterfalls. Its most extensive exposure occurs on the Washington side of the river, where the southeastward dip of its bedding planes has led to many landslides, the largest of which—whose remnants are to be seen at the Cascade Rapids—has received special attention in earlier papers (Lawrence, 1935, 1936, 1937).

Over the Eagle Creek formation lies Columbia River basalt up to 3,000 feet in thickness. This is a basic lava representing the series of lava flows

that covered much of the present states of Oregon, Washington and Idaho, probably in Miocene time (Piper, 1932). Of the score of separate flows of this formation that are visible in the gorge (Smith, 1917), many of the thinner ones are characterized by coarse columnar structure, while the thicker ones frequently show coarse columnar structure below and non-columnar structure above; the columns when present are usually oriented vertically and the whole formation exhibits a pronounced tendency toward vertical fracture. To these characteristics may be attributed the many spectacular pinnacles and turrets that line the gorge walls. Over the vertical and overhanging cliffs of this basalt formation tumble most of the tributary streams that enter the gorge.

Next above the basalt lies the Satsop formation of Bretz (1917) and of Williams (1916), which is probably correlated with Buwalda and Moore's (1930) Hood River formation, Piper's (1932) Dalles formation, and part of Hodge's (1932) Madras formation. The Satsop is seen throughout the gorge and is composed largely of layers of gravels, sandstone, and ashy shales, except in the region adjacent to the Cascade Rapids, where it is composed of volcanic tuff. It is thought by some students to have been deposited in upper Miocene and lower Pliocene time (Piper, 1932).

On top of the Satsop beds are still other volcanic layers—tuffs, breccias, and andesitic and basaltic lavas—some of which are of comparatively recent origin. They form most of the present rims of the gorge and largely compose the uppermost rock layers of this portion of the Cascade Range.

In addition to these rock formations should be mentioned (a) the local granitoid intrusion represented by Wind Mountain and Shellrock Mountain, which because of its characteristic manner of fracturing and very frequent movement of surface debris, forms probably the most difficult habitat in the central portion of the gorge, and (b) the masses of glacial till that occur near the mouth of the Hood River. The till was formed by an arm of an ancient glacier that extended down to this point from the region of Mt. Hood. Other ancient glaciers may have descended other valleys to the river's edge, but the gorge itself has surely never been subjected to glaciation throughout its length.

THE GORGE SOILS

No calcareous beds of any sort are found within the gorge and its sedimentary deposits are all of igneous derivation. The soils are generally shallow, excepting some areas of relatively deep alluvium on the gorge floor. As might be expected from the volcanic origin of most of their mineral constituents, the soils of the gorge seem to be characterized by a notable chemical uniformity; they are in general well provided with the minerals necessary for plant growth, and alkali soils are apparently absent. As to physical characteristics, water-holding capacity, and drainage, the soils vary throughout a very wide range; clays, silts, loams, and sands are all to be

found, usually with only a thin surface admixture of humus; but in places flat enough to accumulate plant remains, patches of predominantly humus soil have been formed. Soils of the slopes contain various amounts of rock debris and these soils naturally differ according to the nature and particle-size of the mineral material contained. Soil influence upon the plant life of the gorge is apparently mainly effective through water relations, or through relations dependent on soil aeration—which, in turn, depend largely on water content. Upon water relations are dependent most of the soil characteristics that differentiate the many widely various plant habitats of the gorge and furnish opportunity for the growth of such an extensive range of life forms as are found here in relatively close proximity.

Naturally the depth of soil is, in general, greatest on the gorge floor, especially in the stretch above the rapids, and it is generally least on the walls of the gorge. Much of the walls and large areas of the floor are of rock that is nearly or quite bare. In crevices, niches, and hollows of the exposed rock have accumulated restricted soil masses, in which many plants grow. The soil of cracks and crevices is usually finely powdered black humus, derived largely from lichens and mosses, which holds water in large volume and with great tenacity.

On the gorge floor the deep alluvial sands, silts, and clays are kept very wet by natural sub-irrigation throughout a large portion of each year and, judging from the character of their vegetation, are apparently more or less acid. Here the moisture supply for plant growth is never deficient, but the oxygen supply may be a limiting ecological condition in many places.

Dunes occur on the gorge floor in the extreme eastern part and also near the western end. In the east, where the climate is dry, the sandy material from the river flood plains, shifted by the strong west winds of summer, fails to become well anchored by vegetation and here the dunes are of the moving kind—many of them typically crescentic in shape. They form a continual hindrance to the railroads of that region. The dunes of the western part of the gorge, formed by the strong east winds of winter, are usually quickly fixed by plants during the growing season, for precipitation is abundant here. As a result of these striking differences in moisture and in seasonal distribution of the winds, the dunes of the west portal are far less conspicuous than those near the other end of the gorge.

GENERAL VEGETATIONAL FEATURES OF THE GORGE

VEGETATION TYPES

Within its fifty-five miles of length and its average breadth of about five miles, the Columbia Gorge presents a remarkably interesting range of vegetational characteristics. It constitutes a sort of transition corridor through the barrier of the Cascade Mountains, connecting hydric evergreen forest on the west with the microphyll desert of the Columbia Basin on the

east (Shantz and Zon, 1924, Shreve, 1917)—a transition due chiefly to such general climatic differences as correspond to a marked diminution in the intensity of rainfall and cloudiness from west to east and to an equally pronounced increase in the intensity of summer evaporativity and solar radiation in the same direction. The west-east range of vegetation types is nearly equalled in diversity and extent by the range from rim to rim. The latter is related to diverse conditions of soil and drainage, to various inclinations of slope, to differences in elevation, and to differences in climatic influences such as those of evaporativity and solar radiation.

Piper's (1906) excellent classification of the vegetation types of Washington—which is a modification of Merriam's (1894, 1898) well-known general scheme of life zones of the United States generally fits to an admirable degree the regions adjacent to the gorge, such as the Willamette Valley, the Cascade Mountains, and the Columbia Basin; but within the gorge itself plants that are elsewhere restricted to different life zones may often be found growing close together. Piper's Humid Transition zone is well represented on the walls of the western part of the gorge, where the characteristic appearance of the vegetation is principally due to Douglas fir (*Pseudotsuga taxifolia* [Poir.] Britt.), which is accompanied by giant arbor vitae (*Thuja plicata* D. Don), red alder (*Alnus oregana* Nutt.), Oregon maple (*Acer macrophyllum* Pursh), and a large number of shrubs. The Timbered Arid Transition zone of Piper is represented by many areas in the eastern part of the gorge, especially on slopes near the east portal that are partly protected from direct radiation; there ponderosa pine (*Pinus ponderosa* [Dougl.] Lawson) is the most conspicuous tree, but Garry oak (*Quercus garryana* Dougl.), which is more characteristically found in the drier portions of the Humid Transition zone, is also abundant. Piper's Treeless Arid Transition zone is represented by exposed areas in the eastern part; it is there characterized by bunchgrass (*Agropyron spicatum* [Pursh] Scribn. and Smith). His Upper Sonoran zone is represented in the Columbia Basin east of the gorge, where the most conspicuous plants are sagebrush (*Artemisia tridentata* Nutt.) and antelope brush (*Kunzia tridentata* [Pursh] Spreng). In the mountainous regions north and south of the middle reach of the gorge, and not very far from its rims, are typical examples of Piper's Canadian, Hudsonian, and Arctic vegetations but, except to note that a number of their characteristic species descend to low elevations in the gorge, these zones are not included within the purview of this study.

As might be expected, the vegetation types and plant communities of the gorge are clearly controlled in large part by conditions of climate and soil. Climate is very different on the two sides of the Cascade Range and the difference is reflected in the gorge; westward from the mountain axis, which is approximately marked by Wind Mountain, the climate is characteristically moist, while eastward from that point it is much drier. This

probably accounts for most of the main vegetational differences between the western and eastern portions of the gorge.

Soil-moisture conditions in the gorge are partly controlled by drainage features, such as soil porosity, soil depth and height above the level of the river, and partly by amount and time-distribution of precipitation, evaporativity, and solar radiation. On account of pronounced differences between the north and south walls with respect to impinging solar radiation, the vegetation is correspondingly different on the two walls. In some instances mechanical wind effects, as well as wind influence on evaporativity, differ greatly on the two opposite sides.

HABITATS OF THE GORGE

Although it is difficult to picture a series of plant communities satisfactorily without reference to specific locations and habitats, still a rough idea of the vegetational diversity of the gorge may be obtained if the gorge habitats are grouped to form the four classes characterized below, a few conspicuous or dominant plants being mentioned as examples in each instance: (a) habitats of the gorge floor, (b) habitats of the south wall, (c) habitats of the north wall, and (d) habitats of the uplands adjacent to the rims.

a. *Habitats of the floor.*—The relatively level floor of the gorge is naturally composed partly of the present flood-plains, the major portions of which are usually under water for several weeks in late spring or early summer but whose higher parts may have been submerged only rarely, and partly of areas that show no evidence of having been reached by freshets within the last century or more.

The present flood-plains are largely of clayey soil, which is generally moist and poorly aerated even in the dry season. On them are found such trees as cottonwood (*Populus trichocarpa* T. and G.), ash (*Fraxinus oregana* Nutt.) and willow (*Salix fluviatilis* Nutt., *S. argophylla* Nutt., *S. sessilifolia* Nutt., *S. lasiandra* Benth.); the complete absence of coniferous trees is a notable feature of these plains in general. As to agriculture, these clayey soils are devoted to truck gardens or to the production of alfalfa hay in the east and to dairy-farming in the west.

Within these clayey areas of the plains there occur restricted patches of well-drained soil, of gravel or roughly broken rock fragments, which are usually drier and more thoroughly aerated than the clay, excepting at freshet time. On such patches may be observed a peculiar mingling of typically flood-plain and upland trees, generally including cottonwood, willow, black haw (*Crataegus douglasii* Lindl.), western choke cherry (*Prunus demissa* [Nutt.] Walp.), and occasional trees of Garry oak; where flooding has been least frequent a few Douglas firs are found on these soils in the western portion of the gorge, and a few ponderosa pines in the eastern portion.

Those parts of the gorge floor that lie above the level of the regular freshets of recent years include remains of very ancient flood-plains of

clayey soil, also occasional small sand dunes and restricted rocky areas. On the remnants of ancient flood-plains are found a mixture of lowland and upland forms, such as cottonwood, willow, and Oregon maple—with Douglas fir frequent in the west and ponderosa pine in the east. Such areas are largely devoted to agriculture, being principally used in the west for hay, fodder, and pasture, and in the east for garden truck, apples, pears, and apricots. The dunes are found only at the west portal and in the far eastern portion of the gorge, as has been said. On them cottonwood and black haw are generally conspicuous, and sand dock (*Rumex venosus* Pursh) is characteristic. The rocky areas of the gorge floor bear trees and shrubs that characterize the adjacent gorge walls, also a number of herbaceous plants that appear to have spread westward from the dry region east of the gorge such as *Eriogonum compositum* Dougl., *Sisyrinchium grandiflorum* Dougl., and several grasses of xeric nature.

b. Habitats of the south wall.—The habitats of the gorge walls generally are soil-covered slopes and benches, taluses, cliffs, or ravines. In the west, the soil-covered areas of the south wall—unless in agricultural use—are occupied partly by virgin or second-growth forest and partly by logged-off or burned forest remains. In these forests are found Douglas fir, giant arbor vitae, hemlock (*Tsuga heterophylla* [Raf.] Sarg.), vine maple (*Acer circinatum* Pursh), blue elder (*Sambucus glauca* Nutt.), Oregon maple, hazel (*Corylus californica* [A.DC.] Rose), dogwood (*Cornus nuttalii* Audubon), and Scouler willow (*Salix scouleriana* Barr.). In the east the soil-covered parts of the south wall are occupied largely by ponderosa pine and Garry oak, with occasional Douglas firs, Oregon maples, hazels, and blue elders. The few small areas of this type that are in agricultural use are devoted to fur farming, grazing, and to orchards of apple and pear in the west and mid-gorge regions. In the vicinity of the Hood River Valley orchards of apple, pear, and cherry are very numerous; farther east grazing is more common and only a few small orchards occur.

The taluses of the south wall are generally almost barren of trees and shrubs but their rock surfaces are mostly covered with various lichens; in the west they bear also drought-resistant mosses and *Selaginella rupestris* [L.] Spring, with rock brake (*Cryptogramma acrostichoides* R. Br.) in the crevices.

Permanent waterfalls and wet or moist cliffs occur in the gorge almost exclusively west of the region of the Hood River and are especially numerous on the south side. The moist cliffs are generally richly covered with herbaceous forms, including the seed-plants *Sullivantia oregana* Wats., *Arnica amplexicaulis* Nutt., *Dodecatheon dentatum* Hook., *Senecio harfordii* Greenman, *Bolandra oregana* Watts., *Mimulus alsinoides* Dougl., *Oxalis oregana* Nutt., and *Saxifraga rufidula* [Small] Piper. Western maidenhair fern (*Adiantum pedatum aleuticum* Rupr.), *Selaginella douglasii* [Hook.]

Spring and many moisture-loving mosses are usually found here in great abundance. On the other hand, cliffs that are not kept moist most of the time bear a very different kind of vegetation, with fewer species as well as fewer individuals. Among the characteristic plants of these drier cliffs, especially toward the west, are *Penstemon rupicola* [Piper] Howell, *Campanula rotundifolia* L., *Sedum spathulifolium* Hook., and *Saxifraga bronchialis vespertina* [Small] Rosend. Toward the east end of the gorge *Penstemon richardsonii* Dougl., *Eriogonum compositum* Dougl., and *Haplopappus resinosus* [Nutt.] Gray are conspicuous.

The ravines of the south wall are generally filled with vegetation, which is of course more dense in the western portion than in the east. In the west, red alder is one of the commonest trees of these ravines; generally associated with it are Douglas fir, giant arbor vitae, Oregon maple, vine maple, and the shrubs ninebark (*Physocarpus opulifolius* [L.] Maxim.), red elder (*Sambucus callicarpa* Greene), and stink currant (*Ribes bracteosum* Dougl.); less common are devil's club (*Echinopanax horridum* [J. E. Smith] Dec. and Planch.) and Oregon yew (*Taxus brevifolia* Nutt.). In ravines near the eastern end of the gorge, which are generally relatively dry, are found Garry oak and ponderosa pine, together with species that grow abundantly on open walls farther west—Oregon maple, hazel, blue elder, and occasionally Douglas fir and dogwood.

c. Habitats of the north wall.—Because the north wall of the gorge generally receives much more solar radiation than the south wall, the two walls differ strikingly with respect to vegetation. The difference is usually

FIG. 2. Eastern portion of the Columbia Gorge; view east from Mayer Park, Oregon. August, 1933.

most pronounced in the eastern portion (see Fig. 2). Here the growing season is much less favorable for plant growth in general than it is anywhere else, because summer sunshine and summer evaporativity are most

intense and summer precipitation is least, therefore local climatic differences are most clearly reflected in the vegetation.

In the western portion of the gorge burned-over areas are notably more extensive on the north wall than on the south wall, doubtless because the former is generally drier than the latter. Also some herbaceous species that are occasionally found on the drier north wall in the west have not been recorded for the more humid south wall except in the east. Gorman (1920) lists ten such species occurring on Hamilton Mountain (see Figs. 1 and 5) in the western part of the gorge. Indigenous to the semi-arid region of eastern Washington and Oregon, these appear to have migrated far westward on the drier north wall. They have been observed on the south wall only near the eastern portal. In the heart of the Cascade Range the vegetational difference between the two walls is emphasized by the difference in the relative abundance of ponderosa pines as compared with Douglas firs. Here, on the north wall many ponderosa pines occur among the firs, while on the south wall just opposite, the pines are absent. Ponderosa pines are not found in the western part of the gorge; there Douglas firs dominate both walls. In the eastern part between Hood River and Lyle pines appear conspicuously on both walls and probably exceed the firs in abundance. As one proceeds eastward from the middle of the gorge into the less humid region, the fir is seen to become progressively less frequent and east of the White Salmon River it fails altogether on the north wall. East of Lyle the north wall is essentially without either trees or shrubs. On the other hand, trees are still numerous on the south wall near the eastern end of the gorge, the dominant forms being oak and pine, with occasional firs and maples.

As to agriculture, suitable areas of the western north wall are used for orchards of prune, apple, and pear, and are occasionally devoted to grain. In the vicinity of the White Salmon Valley, apple and pear orchards are very common but still farther eastward agriculture is confined to grazing and a small amount of wheat culture.

The vegetation of the talus slopes of the north wall is similar to that occurring on similar slopes on the south wall, but it is notably more sparse on the Washington side.

With respect to their vegetation, the fewer moist cliffs of the north wall are not very unlike the more numerous ones of the south wall. *Sullivantia oregana,* which is common or frequent on southern moist cliffs (with northerly exposure), is very rarely found on moist cliffs of the north wall (with southerly exposure); *Saxifraga bronchialis vespertina,* which is characteristic of dry cliffs on the south wall, seems to be less abundant on the cliffs north of the river.

Ravines of the north and south walls in the western part of the gorge are similar with respect to vegetation, but east of the Klickitat Valley fewer

species of shrubs and trees, and fewer individuals of these, are found in the northern than in the southern ravines. In the northern ravines Oregon maple, Garry oak, hazel, and blue elder appear much dwarfed when compared with the same species as they occur in ravines of the opposite wall and on open slopes of both walls farther west.

d. Uplands adjacent to the gorge rims (see Map Citation No. 1).—North and south of the western and middle portions of the gorge the uplands—when not burned or cut over—are generally heavily timbered at elevations of from 1,000 to 3,000 feet, with a forest that contains immense specimens of Douglas fir, hemlock, and giant arbor vitae. At higher elevations, from 3,000 to 5,000 feet, as far east as the White Salmon Valley on the Washington side and a little beyond the Hood River Valley on the Oregon side, the characteristic trees are noble fir (*Abies nobilis* Lindl.), amabilis fir (*Abies amabilis* [Dougl.] Forbes), and western white pine (*Pinus monticola* Dougl.). Eastward from the regions just mentioned, ponderosa pine is the conspicuous tree of the uplands, which are here generally lower than 3,000 feet, but the upland forest is seen to be progressively more open as the observer approaches the east portal of the gorge. In the vicinity of that portal, especially south of the river, the upland is largely treeless, bearing predominantly grasses and thickets of scrub oak.

The cleared uplands of the western gorge region are used for raising grain, for small orchards, and for grazing of dairy cattle. A recently introduced and highly successful agricultural industry here is the production of narcissus bulbs. The valley of the Hood River and that of the White Salmon River have been artificially irrigated for many years, being intensively devoted to apple, pear, and cherry orchards up to an elevation of about 2,000 feet. Eastward beyond these valleys orcharding is also practiced on the south side of the Columbia, but by the methods of dry-farming. Elsewhere in the region of the eastern gorge the cleared or naturally open uplands are used for wheat growing and for grazing.

THE GORGE AS CORRIDOR AND BARRIER

It is apparent that the gorge has served as a sort of corridor for plant migration from east to west and from west to east through the great barrier of the Cascade Mountains, and migration is surely continuing. As examples of migrants from east to west may be mentioned sand dock, sumac (*Rhus glabra occidentalis* Torr.), large-flowered clover (*Trifolium macrocephalum* [Pursh] Poir.), *Penstemon richardsonii* Dougl., *Anogra pallida* [Lindl.] Britt., and *Piscaria setigera* [Hook.] Piper. Mainly confined to the very dry and treeless region east of the gorge, these species are frequent within the east portal, and they are sparingly found farther westward; the Piscaria occurs even beyond the west portal. In the more humid region these forms occur on dunes adjacent to the river, except for the clover and the Penstemon, which grow only on dry ridges and in dry shallow grottoes

in cliffs, respectively. Among the plants that appear to have spread from west to east are Oregon ash, Garry oak, Oregon maple, vine maple, dogwood, and Oregon grape (*Berberis aquifolium* Pursh), which belong ecologically to the western humid region but occasionally occur as far east as the vicinity of the east portal.

On the other hand, there seems to be evidence that the gorge may have acted as a barrier to hinder the northward or southward spread of some plant forms. For example, *Castanopsis chrysophylla* [Dougl.] A. DC., *Delphinium trolliifolium* Gray, *Erigeron howellii* Gray, and *Sullivantia oregana* are almost completely confined to the Oregon side, while *Ranunculus triternatus* Gray, and *Penstemon variabilis* Suksd. occur on the Washington side but have not been reported from the Oregon side.

FLOOD TOLERANCE OF LIVING FIRS AND PINES ABOVE THE CASCADE RAPIDS

Although, as has been said, coniferous trees are entirely absent from the frequently inundated areas of deep silt on the gorge floor, which, as far as trees are concerned, are exclusively occupied by willows, ashes, and cottonwoods, yet a few healthy Douglas firs and ponderosa pines occur below the level of the highest floods in the region east of Cascade Locks. These exceptional trees are found only on occasional small areas of gravel or broken rock, which become much more quickly drained than the neighboring silt areas as each spring freshet recedes. In the summer of 1935 and with the aid of Elizabeth G. Lawrence, a number of firs and pines growing nearest to the level of the river surface on some of these gravelly or rocky areas were studied with reference to the elevations of their upper roots above mean sea-level and to the flood records, which for this part of the gorge are continuous since 1879.

A thorough search along both shores of the river eastward for 25 miles from Cascade Locks revealed only a few firs whose upper roots could possibly have been submerged at any time of their lives. Of the firs examined, the three growing nearest to the river level were young trees, the oldest being probably not more than 35 years of age. According to the flood records, the land upon which these trees stand had never been entirely submerged since the June flood of 1894; consequently the roots of these trees have never been submerged.

Five much larger and older firs, growing at somewhat higher elevations in as many different places, had surely had their roots submerged within the period of the flood records. The lowest of these trees, which was about 130 years old, had had its root system totally submerged only once in the last fifty-five years of its life; namely, in June, 1894, when its root system must have been completely under water for about two weeks. It appears that Douglas fir in this region cannot tolerate prolonged or frequent inundation of its roots.

On the other hand, ponderosa pine (which is not found in the gorge west of the Cascade Rapids) appears to be remarkably tolerant of flooding. Fifteen individuals of this species were found growing so near to the river level that their roots must have been flooded at least seven times in the past 55 years. The root system of the lowest-growing of these, which was about 100 years old, was about 11 feet lower than that of the lowest-growing fir. The flood records indicate that freshet water had stood above its upper roots 29 times in the last 55 years, that on 10 of these occasions the entire root system must have been submerged for at least 2 weeks, and that in 1894 it was submerged for over a month. Figure 3 shows the base of this particular tree. Its upper roots are largely exposed, through wave action at flood times, and pieces of driftwood lying about furnish additional evidence that this tree must have survived at least a number of floodings.

Near this lowest-growing pine stood several Garry oaks about 20 years of age, which were apparently in good health although their uppermost roots were at levels 5 or 6 feet lower than the upper pine roots, where they must have been flooded many times. It is thus evident that this oak also is highly tolerant to repeated flooding in this region of the gorge.

When a plant is killed as a result of the flooding of the soil about its roots the lethal influence may be directly or indirectly attributed to inadequacy of soil aeration—to inadequacy of oxygen supply to the roots—or to effects produced by micro-organisms in the water-saturated soil. Trees are often killed by piling soil about them in grading operations, even when no flooding occurs, and the injurious effect of such burying is also to be attributed to deficient aeration of the soil adjacent to the roots. In his study of oxygen-supplying powers of soils, Hutchins (1926) found that oxygen supply was almost completely stopped by a 16-inch layer of wet, firmly packed loam. That Douglas fir is unable to tolerate much flooding is indicated clearly by the indirect evidence presented above, and the writer has seen several trees of this species killed within a year as the apparent result of piling clay around them to a depth of 3 feet or less, although the added soil was kept away from the trunks for about a foot. It appears that this fir requires a rather plentiful supply of oxygen in the soil about its roots—a more abundant supply than is required by ponderosa pine and a much more abundant supply than is requisite for Garry oak.

That different plant species exhibit marked differences in their responses to the flooding or burying of the soils in which they are rooted is commonly known, but quantitative information concerning the penetration of oxygen into the soil and the oxygen requirements of plant roots seems to be very limited indeed. Free (1917) and Livingston and Free (1917) reported that potted plants of a willow known to thrive in very wet soils remained healthy for 10 months without any oxygen supply to their roots, excepting what might be delivered internally through leaves and stems; on the other

FIG. 3. Base of ponderosa pine near Collins, Washington, showing effects of floods. August, 1935.

hand, their plants of Coleus and Heliotropium wilted promptly when the air of the soil about their roots was replaced with oxygen-free nitrogen. Bergman (1920) subsequently found that flooding the soil in which plants of Coleus and Pelargonium were growing caused the leaves of these plants to turn yellow and to drop off in about two weeks. Potted plants of *Coleus blumei* showed signs of wilting one or two days after their roots had been submerged. But when the water with which these roots were flooded was adequately aerated the plants did not wilt, but remained in good health as long as artificial aeration was maintained. With regard to their soil-oxygen requirements, it appears that the willows, cottonwood, and ash of the Columbia Gorge flood-plain may be similar to the willow plants of Livingston and Free's experiments, that Douglas fir may be similar to the Coleus, Heliotropium, and Pelargonium plants of those authors and of Bergman, and that ponderosa pine and Garry oak may be intermediate.

ASYMMETRIC CROWNS AND THEIR RELATION TO WIND AND WEATHER IN THE GORGE

THE ASYMMETRIC CROWNS

Introduction.—In Pacific Coast forests the Douglas fir trees are usually more or less nearly symmetrical as is the tree shown in Figure 4. Such symmetry of crown form is rarely to be seen, however, as one travels eastward from Portland to the treeless region of the Columbia Basin through the 60 miles of rugged and timbered Columbia Gorge; there, in the gorge, one is impressed by the remarkable one-sided crowns that characterize the needle-leaved trees in the western and eastern portions.

From Crown Point, at the lower end of the gorge, the splendid view extends about 25 miles up the river in a northeasterly direction, to Wind Mountain, in the heart of the Cascade Range. An idea of this view may be had from the photograph of Figure 5 which was obtained by means of dark red and infra-red rays only. Throughout this nearly straight stretch many of the fir trees that line the gorge are remarkable because of their conspicuous one-sided crowns; for almost all of their large branches extend in a westerly direction from the trunks. The gorge bends slightly toward the east where the first view terminates and, as one proceeds around the bend, it is soon noticed that the asymmetric fir trees seem to have faced about, with their larger limbs extending toward the east instead of toward the west. (Note the tree symbols on the map of Fig. 1.)

A widespread popular idea or belief is offered by dwellers in and near the gorge, in attempted explanation of this striking difference between the fir crowns east and west of the bend. According to this erroneous idea, the winds of the gorge, which are wrongly supposed to arise in the valley of the Wind River, first swirl about Wind Mountain and so become separated into two winds of opposite direction, which then pass forth from that region,

FIG. 4. Symmetrical Douglas fir near Portland, Oregon. (G. C. Stephenson, photo.)

simultaneously eastward and westward; a statement often made is that "the prevailing winds blow outward from the center of the gorge." That what appear to be cloud swirls are sometimes seen about the summit of Wind Mountain seems to lend a kind of support to this popular idea about the origin of the gorge winds; but that idea is wholly erroneous, for weather rec-

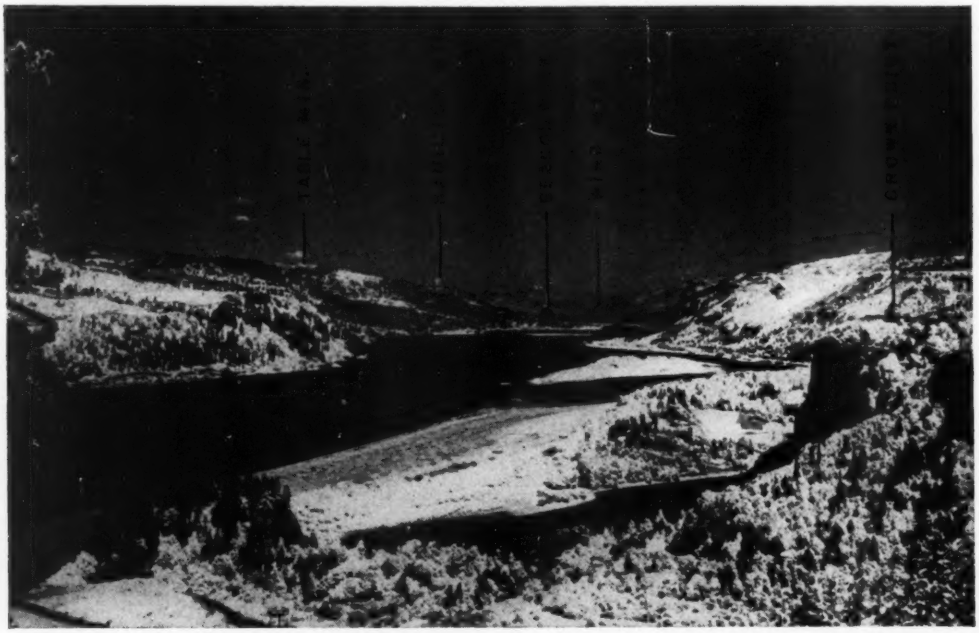

FIG. 5. Western portion of the Columbia Gorge; view northeast from near Chanticleer Point, Oregon, photographed with dark red and infra-red rays only. August, 1934.

ords show that at any one time the general trend of wind movement is continuous through the whole gorge, either eastward or westward from one portal to the other, and wind velocity generally increases greatly from the portal of entrance to the portal of exit. Although the deformations of the firs are indeed due primarily to wind influence, yet the relations actually involved are far too complex to be appreciated except through detailed examination of the trees themselves at different seasons of the year and through analytical study of the meteorological records of the gorge. Results of such examination and study are presented in the present section.

That this problem concerning the one-sided tree crowns of the Columbia Gorge has not previously been very thoroughly studied may have been largely due to the fact that access to many parts of the gorge has only recently been rendered relatively easy and inviting, through the development of automobile roads. Furthermore, the meteorological and climatological aspects of the problem could not be satisfactorily studied until within the last few years because the requisite meterological records and facilities for studying the weather of the gorge were not available.

Very satisfactory weather records for the gorge region, collected in the period since 1929, are now available, however, in the office of the Portland Municipal Airport, and free access to them was had through the friendly co-operation of Mr. J. C. Smith, of that office. Mr. Donald C. Cameron, formerly of the same office, has helped the writer very much in the study

of the gorge winds. Much was gained also by prolonged studies of current meteorological observations as these were recorded on the teletype ribbons at the four meteorological stations within the gorge. These airway weather-reporting stations (of the United States Weather Bureau and the United States Bureau of Air Commerce) are about twenty miles apart, one being close to each portal of the gorge while the others are respectively near Cascade Locks and Hood River. (See the circled triangles on the map of Fig. 1.) Simultaneous hourly notes on atmospheric conditions at all four stations are promptly shown at every one of them; thus, at any time, day or night and at any station, one may study the current weather conditions throughout the gorge and follow weather changes, as they proceed. Through the courtesy of the resident observers, many pleasant and helpful hours were spent in that way.

Fir crowns of the western part.—The western type of fir crown deformation, in which most of the large branches project in a westerly direction from the trunks, is most strongly developed near the west portal of the gorge. Extreme examples from that region are shown in Figures 6 and 7. Observed in late summer near the end of the growing season the one-sided trees here present a characteristic rigid, tattered, and grotesque appearance. Their trunks stand nearly upright or lean a few degrees toward the west, but all are essentially straight. The crowns are usually narrow and spire-shaped, with many dead limbs and conspicuous jagged fragments among the longer branches. Much of the apical portion of the crown, for two feet or more back from the tip, is generally without foliage and appears bleached and weathered, as is seen in Figure 7. The rest of the crown is almost wholly confined to a vertical segment on the west side, which represents only about a quarter of the usual symmetric conical crown of an undeformed Douglas fir (compare with Fig. 4), but even within that segment, the branches are relatively short. They are generally covered with dense tufts of foliage twigs, irregularly distributed along the proximal parts of the branches while the distal portions often lack foliage entirely; the longest branches are sometimes completely bare and dead, as may be seen in Figures 6 and 7. When branches occur on the north and south sides of the trunk these show much evidence of pruning, with broken tips; and areas of sparse foliage and densely bunched foliage twigs occur in alternate regions of the branch. On the east side, where there are no long branches, short branch stubs, about four inches long, show that branches of from one to six years' growth have been broken away. Sometimes the outer portion of a longer branch still hangs leafless from its stub by a shred of wood. But this eastern side of the bole is usually densely clothed with short, vigorous branchlets and twigs of the last one or two seasons, which form a thick leafy mantle that often completely hides the middle region of the trunk on that side. These short branchlets and twigs extend outward from the trunk generally not

more than about 6 inches, appearing as though clipped by a gardener's shears. In the lower portion of the crown, where the eastern mantle of branchlets is often incomplete or lacking, the trunk on that side is apt to be studded with fungous conchs and gnarled knots, where branch stubs have healed imperfectly. On the ground are to be seen the more or less completely decayed remains of the branches whose stubs are so conspicuous above.

Such summer observations make it evident that these trees must have been subjected to a very drastic natural pruning, effective especially on the east, less on the north and south and only slightly on the west. It is clear that this pruning must have occurred at some other season of the year, for it is obviously not in progress in summer. Furthermore, summer wind in the western part of the gorge is usually gentle and from the west; east winds at this season are rare and are not strong enough to cause the breakage of branches.

But east winds of excessive velocity do occasionally occur here in winter and these are sometimes accompanied by the freezing rain of very destructive glaze storms, which are locally called "silver thaws." Although winter gales without ice deposition sometimes cause considerable breakage of branches and trunks due to wind pressure alone, most of the drastic pruning just described is brought about by the combined action of the east wind and massive ice deposits on the trees.

The writer has not made extensive observations of the deformed trees here considered in the winter season but it is reported by Mr. Donald C. Cameron and by the official weather observer at Crown Point, Mr. William A. Johnson, that when the trees are examined shortly after the close of a glaze storm many newly fallen branches with green foliage still in place are to be found on the ground about the trunks and freshly formed stubs from which these branches have been broken very recently are also to be observed. Injury is most pronounced in the upper portions of the crowns and on the east and northeast sides of the trees; some breakage has usually occurred on the north and south sides but evidence of breakage is rare on the west sides. Although the effect of the glaze deposit on the dense mantle of short living branches and foliage twigs on the east side of each trunk has not been directly studied, the mantle probably remains essentially intact since it should be largely protected throughout the most severe part of the storm by a more or less complete covering of ice.

In addition to this one-sided storm-pruning to which these Crown Point firs are subjected during glaze storms, another form of winter injury occasionally takes place, which becomes manifest only at a much later time and is almost entirely unrelated to those storms. Sometimes when the trees are examined in early spring—in March or April of some years—most of the leaves on the eastern side of the crown, including those borne by the few projecting branches on that side as well as those of the bole mantle, are

found to be dead and discolored, but still in place. At such times much of the east side of the crown is red-brown in color, appearing as though its foliage had recently been scorched by fire. This kind of delayed evidence of winter injury has been called "parch blight" by Munger (1916), who studied it in the vicinity of Portland as well as in the western part of the gorge. Near Crown Point it sometimes embraces the whole apical region of the crown for a distance of several feet from the tip. Farther down, the parch blight discoloration is incomplete and less pronounced on the northern and southern sides of the crown, but it is apt to include the longer branches even on the western side, where it is least evident. The tallest trees are most affected and the younger ones of a group frequently show little blight injury except on their eastern sides. When Munger's parch blight is observed in early spring the dead leaves are still in place but, as they fall off and the new foliage twigs and new leaves expand, the trees once more assume their normal green color.

This kind of injury is sometimes very severe. Trees that have been exceptionally exposed to the winter winds are in some cases killed outright, especially if the soil at their bases is unusually shallow. But parch blight does not occur every spring and it is seldom observed in consecutive springs; thus the injured trees usually have two or more growing seasons for recovery before they are again subjected to injury of this sort. It is consequently understandable how the fir forest of the western gorge is able to persist in spite of occasional drastic storm-pruning and extensive spring defoliation. The relations between these two forms of injury and winter weather will receive attention farther on.

Fir crowns of the eastern part.—Extreme examples of asymmetric firs of the eastern part of the gorge, with all branches extending eastward from the trunks, may be seen near Mitchell Point or near Ortley Point, which are respectively 35 miles and 53 miles east of Crown Point (see Fig. 1). Some of these trees are shown in Figures 8 and 9. They differ from the western ones not only in the direction of their asymmetry but also in other notable ways, especially in that they appear to be wind-trained rather than storm-pruned. They resemble to some extent wind-swept trees sometimes seen near the sea-shore but they are not at all dwarfed or gnarled. The trunks are commonly bowed slightly toward the east, especially above, and their slender tips are frequently strongly bent in the same direction, each one forming a graceful curve that may terminate in a line that departs as much as 30 degrees from the vertical. Leafless or dead branches and stubs of broken branches, which are so characteristic of the Crown Point trees are uncommon here, nor is there at any time of year any evidence of parch blight in these eastern trees. The boles are characteristically smooth, rarely marred by any evidence of injury of any sort, and the short branches and foliage twigs do not form characteristic dense trunk mantles such as are

common on the eastern sides of the Crown Point trees. Numerous well-developed leafy branches, in excellent health, arise from all sides of the trunk, but those arising on the western, northern, and southern sides have been sharply bent around, so as to extend eastward along with those arising from the eastern side. Almost every long branch droops slightly but it is gently bowed upward toward its tip. The crown is thus essentially confined to a vertical segment representing little more than one-sixth of the cone represented by the crown of a symmetrical, undeformed tree (compare with Fig. 4). The origins of the older branches from the west side are commonly so overgrown, through bole enlargement, that the basal portions of their bends are concealed, and these bent branches consequently appear to arise south or north of their real origins.

The crowns of these eastern trees have obviously been molded by wind pressure alone; they have not been trimmed or pruned by breakage, as have their fellows at the western end of the gorge. Essentially free from breakage or lethal injury of any kind, they have been, as it were, trained into shape by persistent and powerful west wind which must have acted during the growing season rather than in winter. In the eastern part of the gorge such winds are indeed prevalent in late spring and in summer, especially by day—when the growing tissues of the fir branches are most readily bent by wind pressure.

The peculiar asymmetry of these eastern fir crowns, as contrasted with that of the western ones, is best appreciated by reference to Figures 6 to 9. Whereas the western crowns have been deformed by breakage and killing due to the glaze storms and strong east winds of midwinter, the eastern ones have been deformed by long-continued pressure of strong west winds of late spring and summer. It will be noted that the photographs of Figures 6 to 9 and also that of Figure 10, to which reference will be made below—all represent views looking northward; thus they are directly and readily comparable. Comparison of these photographs should bring out additional details concerning the forms and structures of these two very different types of crown.

Fir crowns of the middle region.—From Ortley Point westward, until the bend in the gorge is approached, the one-sided Douglas firs are all essentially similar to those of the eastern end—with wind-trained crowns east of the boles. Westward from the bend the one-sided crowns are like those around Crown Point—battered and broken and extending west of the boles. In the region of transition (which extends about twenty miles on both sides of the river from the vicinity of Beacon Rock to Mitchell Point and the Little White Salmon River) both types of crown are to be seen, also trees in which the two types are combined in various curious and interesting ways. In some instances the well-developed branches extend mainly northward and southward from the boles, both eastern and western sides being relatively

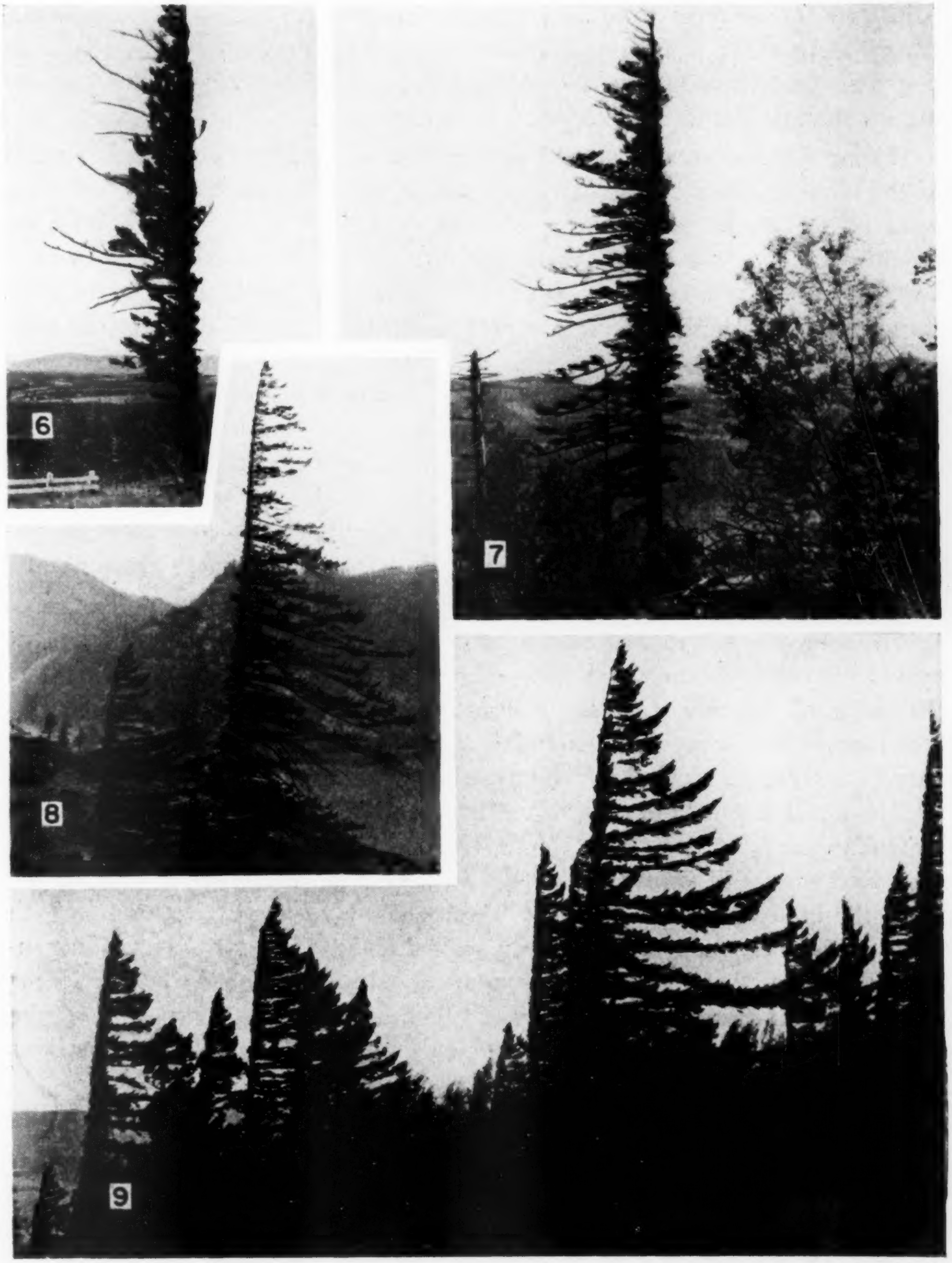

FIG. 6. Storm-pruned Douglas fir near Crown Point, Oregon; seen from the south. August, 1933. FIG. 7. Another Douglas fir near Crown Point, Oregon; seen from the south. May, 1937. FIG. 8. Wind-trained Douglas firs near Mitchell Point, Oregon; seen from the south. August, 1934. FIG. 9. Wind-trained Douglas firs near Ortley Point, Oregon; seen from the south. August, 1934.

free from long branches. In other instances the upper part of the crown conforms to one type while a lower part conforms to the other. And some trees fail to show pronounced deformation of either sort. Signs of parch blight are seldom to be seen in the region of transition except in trees growing on shallow soil in very exposed locations.

From the southern approach to the highway bridge called the "Bridge of the Gods," which crosses the Columbia River at Cascade Locks, near the bend of the gorge, tree crowns of both types are to be seen at once on opposite sides of the river; across the river and about a quarter of a mile away are trees with rugged crowns that extend westward, while in the near foreground on the south side are several graceful wind-blown forms, with crowns extending eastward. From very casual inspection it might appear that both forms might have been produced here so close together by some sort of wind swirl, but such a supposition will not bear scrutiny. The glaze-storm east winds that broke and battered the trees across the river blew in winter and the less harmful west winds that molded the nearby trees blew in summer; local topographic features of the gorge walls at this point apparently have acted to shelter the nearby trees from east wind, blowing down the river, but not from west wind, blowing up-stream.

An interesting combination form of fir crown is shown by a tree that stands on the Government Locks Property, near the eastern boundary of the town of Cascade Locks. It leans toward the east and most of the branches of its lower part extend in an easterly direction, but the upper part of its crown has largely been stripped of branches and the few that remain intact extend northward and southward. The lower portion of the crown appears to have been effectively sheltered from the very injurious east-wind storms of winter and to some extent from the summer west winds, while the upper portion appears to have been about equally exposed to both winds and consequently to have been shaped about equally by both. In general, it appears that the kind of asymmetry exhibited by a fir crown in the mid-gorge transition region is determined by the particular exposure of the tree in question, which seems to depend primarily upon local conditions of wind movement as influenced by local topography.

Other kinds of trees with one-sided crowns.—Because Douglas fir is by far the commonest tree in the gorge and because it occurs plentifully in both western and eastern parts, this tree presents the most striking and continuously consistent picture of crown deformation. For that reason it has been referred to throughout this descriptive account, but other species exhibit similar types of deformation. For example, Oregon maple and Garry oak (see Fig. 10), which are found sparingly throughout the gorge, might profitably be studied in this connection. In the eastern part of the gorge—to which it is confined—ponderosa pine frequently shows crowns deformed by west-wind pressure, which appear very much like the one-sided fir crowns

FIG. 10. Wind-trained ponderosa pines and Garry oak near Crates Point, Oregon; seen from the southwest on a calm day. June, 1937.

of the same region. Such a pine crown is shown by the photograph of Figure 10. Since the foliage of this species is less crowded than that of Douglas fir and since its branches are more rigid, the bending of the latter around the runk from west to east is very conspicuous indeed.

WEATHER CONDITIONS OF THE GORGE AS RELATED TO THE FIR CROWNS

Weather Effects in the Western Gorge

Trunks tilted westward by gales of fall and early spring.—In the western part of the gorge summer weather conditions induce no injury or permanent bending of the fir trees; their conspicuous deformation is produced by conditions that are effective at other times. Summer winds here seldom have excessive velocity, but easterly gales occur in autumn and in early spring and these appear to produce the common westward slant of the fir trunks while the easterly gales and glaze storms of winter are mainly responsible for the one-sided crowns.

Little or no rain falls anywhere in the gorge throughout the summer but in the western part the summer drought ends early in the fall, and heavy rains ensue. Toward the end of September or in early October protracted rain is generally followed by a high east wind, the first fall gale. At Crown

Point its gust velocity may be greater than 40 miles an hour, but it is progressively less violent at stations lying farther up the river and the velocity at Hood River and North Dalles is at that time only about 10 miles an hour or less. This first gale at Crown Point is apt to last two or three days, being generally followed by shorter and shorter periods of gentle westerly breezes, alternating with periods of stronger and more prolonged easterly gales until midwinter, when the maximal east-wind velocities and durations are attained. As the season advances and spring comes on easterly gales become less frequent and less severe, and gentle westerly wind becomes progressively more prevalent. The gales of fall and early spring occur when the soil is unfrozen and has been softened by rain, and wind pressure upon the crown at these seasons tends to loosen and raise the roots slightly on the east side. Consequently the boles lean a little to leeward. This is especially true of the taller and more exposed trees. The gentler winds blowing from the west at these or other times are inadequate to restore tilted trees to the vertical position and they remain tilted year after year as they grow larger. Although the winter gales are stronger than those of autumn and spring and although they also blow from the east, still these are probably not very effective to make the trees lean westward, for they occur when the soil about the roots is apt to be solidly frozen to a depth of 1 or 2 feet, thus furnishing a very firm anchorage.

Destructive glaze storms of winter.—The characteristic glaze storms of the western gorge, to which the one-sided fir crowns of that region are almost wholly due, occur in midwinter or somewhat later. They occur at irregular intervals according to the records, some winters have been characterized by several of them while others have passed without any such occurrence. A glaze storm at Crown Point is regularly preceded by a freezing winter gale without precipitation, which blows through the gorge from the east for a week or longer (Cameron and Carpenter, 1936). Sooner or later, relatively warm coastal air begins to move inland over the gorge from the west, the velocity of the persistent east wind begins to abate and precipitation results. At first this has the form of ordinary snow, accompanied by strong east wind and by slowly rising temperature. At Crown Point the initial snow is apt to change within a few hours into graupel[2] and somewhat later into small spherical globules of clear ice now technically called sleet;[2] these solid particles which are driven westward almost horizontally, at perhaps 30 miles an hour or more may bring about some injurious abrasion of the fir needles and young twigs, especially on the eastern sides of the crowns, but that is probably of no more than minor importance.

After the fall of graupel or sleet has continued for an additional period

[2] *Graupel* and *sleet* are used here in the senses agreed upon by American meteorologists and adopted by the United States Weather Bureau. Photographs and descriptions of these two solid forms of precipitation have been published by Talman (1931). *Graupel* is used to denote frozen precipitation in which the small, rough, nearly spherical particles are white and opaque; the word is derived from the German for pearl barley or groats, and this kind of precipitation is known as "tapioca snow" in the george region.

of a few hours the freezing rain of the typical glaze storm supervenes. Driven by strong east wind, with velocity still not greatly diminished, this precipitation solidifies as it strikes, and it rapidly builds up an armor of ice on trees and other objects. This thickening ice glaze accumulates mainly on the eastern side of each tree, covering every needle and twig of the crown and even the bole itself on that side. As this deposition proceeds the intercepting surfaces become continuously more extensive, and separate portions coalesce to form great masses of ice. The ice surfaces offer increasing resistance to the wind and the ice burden becomes progressively greater on all coated branches and branchlets.

A glaze storm may continue for 24 hours or more, with east-wind velocities between 25 and 30 miles an hour, while branches and twigs on the east and northeast sides of a fir crown may become covered with ice coatings as much as three or four inches thick. Large branches that may have withstood earlier glaze storms, or that may have developed since the last preceding storm of this sort, are apt to be broken and carried away, because of their great ice load and the persistent strong east wind pressure. But, as has been said, the short and crowded twigs of the mantle on the eastern side of each fir trunk probably become completely encased and covered and so must be well protected from wind pressure while their load of ice should be well supported against the bole.

A meteorological description of a severe storm of this kind has been given by Wells (1921). Mr. William A. Johnson, who has been mentioned before in this regard, has kindly furnished the writer with much observational information concerning the glaze storms of the Crown Point region and their effects on the trees, and it seems safe to conclude therefrom and from the observations of other winter residents that most of the drastic pruning of firs of the western part of the gorge occurs in the later periods of such glaze storms. A glaze storm lasting less than twenty-four hours may result in the breakage and removal of branches that have been several years in growing.

As a glaze storm comes to its end the air temperature and the rain become warmer and the east wind abates and is supplanted by gentle southwest breeze. Temperature continues to rise and warm rain continues for several days; consequently the storm ends in a rapid thaw and the ice soon disappears from the trees. During the thaw a little additional breakage is apt to occur through the falling of heavy masses of ice from the upper portions of the trees on to lower branches. Finally, after all ice has disappeared, east wind and clear weather supervene, usually with rapidly falling temperature.

As one ascends the gorge from Crown Point to the mid-gorge region, glaze-storm injury is seen to be progressively less pronounced. But the explanation of this is not to be sought in any marked difference in wind velocity, because the wind velocity of a glaze storm is generally about the same

in the mid-gorge region as farther west. The main reasons are apparently to be found in a notable eastward *increase* in the proportion of total precipitation that occurs in solid form (mostly as snow, but also as graupel and sleet) and in a correspondingly marked *decrease* in the proportion of freezing rain. Thus a glaze storm generally deposits a much more destructive ice load on the trees near Crown Point than on those near Cascade Locks.

From Cascade Locks to the east portal of the gorge the total precipitation accompanying one of these winter storms is progressively less, as are also wind velocity and the thickness of the ice deposit on the trees. Between the east portal and the Hood River both wind velocity and ice formation are so slight that tree injury from these winter storms is neither common nor severe; such injury of this sort as does occur in the eastern region is apt to affect the tree crowns about equally on all sides.

Parch blight induced by drying winter winds with low temperature of air and soil.—Besides the glaze storms just described, the western part of the gorge—and sometimes also the region lying west of the west portal—occasionally experiences cold, drying winter gales lasting a week or more at a time. At Crown Point such gales have velocities of from 40 to 50 miles an hour and on several occasions even hurricanes of 120 miles an hour have been recorded (Cameron, 1931a, 1931b, Cameron and Carpenter, 1936). These pour great volumes of very cold air from the Columbia Basin westward through the gorge. Near the east portal the temperature of the air stream may be as low as –25° F. The air becomes warmer as it moves westward, but near Crown Point its temperature is still well below the freezing-point of water. Its hygrometric deficit naturally increases with rising temperature and its velocity, which is not excessive near the east portal, is also rapidly increased with its progress through the gorge. Consequently at this season evaporativity is not remarkably intense in the east but it is very great in the west. These persistent winds are also often accompanied by bright sunshine in the daytime, which must add very considerably to the pronounced drying influences of excessive hygrometric deficit and excessive wind velocity in the west. It follows that air conditions favoring transpirational water loss from the fir needles and twigs of the Crown Point region must be unusually intense in the periods of these winter gales.

Furthermore, after a week or more of a cold dry gale of this sort, foliage, branches, and trunks must be very cold and their vascular sap may be largely frozen, especially in the more exposed parts. Consequently the conducting power of the tissues that supply the leaves with water must be greatly reduced at such times. This should be notably true even if the sap of twigs and leaf veins should remain liquid, for the viscosity of water increases markedly with decreasing temperature, and the conducting power of these parts must be very low indeed if their vascular sap has been largely frozen. These considerations apply also to large branches and trunks, though perhaps

to a less degree, and to root systems likewise. Turning to the water-absorbing roots, their absorbing power as well as their conducting power must be reduced as soil temperature is lowered. It thus appears that in these periods of winter gales the drying influence of aerial conditions is greatly aggravated while absorbing and conducting powers of the tree itself are greatly reduced at the same time.

As to the water-supplying power of the soil adjacent to the absorbing surfaces of the root system, that may also be considerably or even greatly reduced throughout these periods of intense cold. The capacity of moist soil to supply water to root surfaces must become less as soil temperature falls and it must become very low indeed in so far as the soil in question becomes frozen. Finally, the soil from which water is absorbed by the tree roots may tend to become unusually dry at these times, through evaporation into the air, and any decrease in the water content of a mass of moist soil should lower the water-supplying power of the latter even if soil temperature were not lowered at the same time.

From all of the considerations just suggested it appears that many circumstances accompanying these winter gales conspire to cause the removal of transpirational water from leaves and branches more rapidly than it can be supplied to these parts. This state of affairs naturally leads to unusually advanced degrees of drying. Wherever drying becomes too advanced, leaves, and even twigs and branch tips, are killed and the ultimate outcome is parch blight.

Occasionally in the western gorge are observed fir crowns the upper parts of which project above a sheltering ridge; often the exposed portions of these crowns have been killed by excessive desiccation but the lower portions being effectively protected from the gale remain alive. Cooper (1917) described similar injury of redwoods in the Santa Cruz Mountains of California resulting from desiccation by a strong north wind in spite of the fact that at the time soil moisture was ample. His observations indicated in addition that the redwood is far more susceptible to this type of injury than is the Douglas fir for when the two species side by side had been equally exposed to the wind the foliage of the redwood was dead and that of the fir still alive.

As should be expected, this form of injury in the gorge is most frequently observed on the east side of each affected fir tree, in the upper part of the crown and at the ends of the longer branches, where exposure to the gale has been most drastic; also around the crown from east to southeast, where the sunshine of the early forenoon warms the foliage while the rest of the tree is still at about the air temperature of the preceding night.

As the conditions thus envisaged for the western part of the gorge continue from day to day throughout the period of one of these dry winter gales, the most affected needles on the fir trees of that region die because

of excessive drying. They subsequently lose their original green color, becoming red-brown as spring comes on, but just how much time elapses between the actual death of the needles and the first appearance of the red-brown color is not known. The killed needles usually remain in place till the following midsummer, and in some instances the resulting conspicuous red-brown blotches have been observed to persist in the crowns of parch blighted firs till the dead needles are swept away by gales of the following winter.

Parch blight in the western part of the gorge is apparently not induced to any considerable extent by the east winds of fall and spring presumably because the complex of conditions favoring excessive drying of foliage is at those times much less effective than in the dry gale periods of winter. This form of injury is essentially confined to the western part of the gorge, being almost wholly absent east of Wind Mountain. As has been said, the air movement that produces the dry winter gales in the west is of much lower velocity in the east, and the hygrometric deficit of the moving air becomes excessive only after the latter has been considerably warmed in its westward passage. Also, at the times of these dry winter gales in the western gorge region the weather there is usually clear, while the sky over the eastern part is generally overcast at those times. It is therefore safe to suppose that evaporativity is much more intense in the western part. From Wind Mountain westward, parch blight is progressively more common and more severe, occurring oftenest and most conspicuously in the region of the west portal, near Crown Point.

According to Munger (1916), who studied parch blight in this general region and who gave it its name, the buds adjacent to the blighted fir needles generally open in the usual manner and send forth new shoots the following spring. He noted, however, that many of the branchlets and smallest branches in blighted regions on the eastern sides of the crowns failed to produce spring growth, indicating that they as well as the needles had been killed by the drying-out process. On the whole, parch blight injury does not constitute a very serious menace to Douglas fir, and this form of injury appears to play a secondary part in producing the one-sided crowns of the western part of the gorge.

Munger suggested that the occurrence of parch blight only in the western part, despite the fact that Douglas fir is plentiful throughout the gorge might perhaps be related to hereditary physiological differences between the firs of the two regions. He pointed out that the firs of the eastern gorge have varietal characters resembling those of the Rocky Mountain form of this species, while those of the western gorge are like the less hardy coastal form. Thus the latter might be readily susceptible to this blight injury and the former might generally escape because of a lower degree of susceptibility. Whether the Douglas firs of the gorge really differ with regard to their sus-

ceptibility to the development of excessive water deficit, is of course uncertain, but—as has been noted—the environmental aridity of the eastern part is unquestionably much *less* intense than that of the western part in periods of dry winter gales, when the injury here considered occurs. It may be that even the firs of the eastern gorge might prove just as susceptible to parch blight as are the possibly less hardy ones of the western gorge if both were exposed to the very drastic environmental conditions of the dry winter gales of the Crown Point region.

Weather Effects in the Eastern Gorge

As has been said, glaze storms, which are so largely responsible for crown asymmetry in the western portion of the gorge, are neither common nor destructive in the eastern portion, where east winds are not strong at any season. With the beginning of spring in the eastern gorge, the gentle winds of winter, mostly from the east, give place to persistent west winds, which gradually increase in velocity until maxima of about 30 miles an hour are attained in June and July. These west winds are but gentle breezes in the western part, but their velocity increases eastward and by the time the moving air reaches the middle and eastern region it exerts considerable pressure. After midsummer wind movement declines until fall, when gentle variable and easterly breezes once more prevail in the eastern portion of the gorge.

The effectiveness of the west winds to train the fir crowns in the growing season is enhanced by a sort of daily pulsation, which is most pronounced near the east portal but is evident throughout the eastern region of the gorge. This pulsation occurs to some extent at other seasons of the year, but it is most striking in the growing period, from May to August. The velocity of the eastward air flow increases rapidly each day, from about sunrise on, attaining a diurnal maximum of about 30 miles an hour in the afternoon. It then diminishes gradually and night velocities are often less than 10 miles an hour. This diurnal fluctuation in wind velocity appears to be caused by a sort of large-scale air drainage through the east portal of the gorge into the great open stretches of the Columbia Basin. There the lower air layer regularly becomes greatly heated by sunshine in the daytime, and its consequent rise induces an eastward flow of cooler air from the gorge, thus accelerating the general eastward movement and inducing high velocities by day.

The high daytime wind velocities must be more effective to deform the tree crowns than are the much lower night velocities, although the night winds continue to exert considerable pressure on the branches; the daily maxima of eastward wind pressure occur in those hours when the enlarging young branches and branchlets should be least rigid and elastic, when the turgor of their tissues should be lowest and enlargement and tissue hardening may be nearly or quite at a standstill (Krasnoselsky-Maximov, 1917,

Livingston and Brown, 1912, Maximov and Krasnoselsky-Maximov, 1924). Some recovery from eastward bending may take place at night, but if that occurs it is obviously generally far from complete. In the latter part of the growing season nocturnal recovery may be greatly retarded or prevented because of inadequate water supply, for the soil here is usually remarkably dry in midsummer. Bent strongly toward the east each day by the daytime wind and largely kept bent throughout the night by the less rapid night wind, the branches are wind-trained as they develop. As has been said, the crowns of the eastern gorge show essentially no evidence of breakage.

CROWN ASYMMETRY IN GENERAL AND ITS RELATIONS TO WIND DIRECTION, WIND VELOCITY, AND WIND DURATION

Two distinct types of mechanical wind influence on the trees of the Columbia Gorge.—It appears that the type of crown asymmetry, which is so notably developed in the western part of the gorge, has not before been described as resulting chiefly from glaze injury and it may consequently be presumed that asymmetry resulting from that agent is of rare occurrence. On the other hand, the wind-bent type, which is equally well developed in the eastern part of the gorge, is not uncommon throughout the world; wind deformations of this general sort have been mentioned or described by many writers for many different countries and localities. Both types depend on wind, but the former is produced by a combination of wind pressure and a very peculiar kind of precipitation—i.e., glaze storms—while the latter depends wholly or almost wholly on wind pressure alone.

Characteristics of effective wind.—In order to envisage the general manner in which wind pressure may be effective to produce asymmetric tree crowns it is desirable to consider four different characteristics by which winds differ from time to time and from locality to locality; namely, direction, velocity, and what may be considered as two phases of duration. At any moment, an air current flowing past any station may be satisfactorily defined by stating its direction and its velocity; it may blow from any range of compass points and it may have any velocity from what approaches a dead calm to what constitutes a hurricane. For the sake of convenience in ascertaining the characteristics of effective wind the great range of direction may be reduced to the eight major compass points and the range of velocity may be subdivided into the eight major degrees of intensity recognized by the United States Weather Bureau. In the present brief discussion the vertical component of wind direction may be neglected, air flow being considered essentially horizontal. But since the deformation of tree crowns by wind is not brought about by momentary action, for the present purpose a useful analysis of wind movement at any station must involve two special analyses of wind duration. The first analysis is to characterize the wind in question by showing how long each major degree of intensity of velocity

has been maintained with each major direction of flow, and the second analysis must involve definite reference to both diurnal and seasonal periodicity as it is related to direction and velocity. Furthermore, descriptions of special environmental conditions (such as glaze deposition, low air and soil temperatures, the presence of much salt spray or abrasive material in the air), which occur in various regions at certain times, must supplement the foregoing information. For example, with respect to intensity of velocity and to certain environmental conditions accompanying the wind of any particular direction, the results of the present study indicate that crown deformation in the western part of the Columbia Gorge is almost wholly due to wind of easterly direction, which although it acts for only a small portion of the year is of such great velocity and so coincides with glaze deposition and with low soil and air temperature that it becomes extremely effective in producing tree crown asymmetry. In this western gorge region west wind is the *prevailing wind*[3] for the year but it is not at all effective in this respect.

Another case in point described by Wells and Shunk (1937) shows that salt spray whipped up by winds off the sea make the wind from that direction the effective wind in producing asymmetrical crowns whether or not that is the prevailing wind direction for the year.

A third example, brought out in the present study indicates that crown deformation in the eastern part of the Columbia Gorge is wholly due to winds of summer—when shoots are rapidly elongating and their tissues have not yet become hardened—and that it is largely due to diurnal, rather than nocturnal, winds at that season. As to direction, these effective winds are westerly—as is clear from the compass orientation of the crowns—and their diurnal velocities in summer are of the order of 25 to 35 miles an hour. Nocturnal summer winds and the winds of autumn, winter, and early spring, whatever may be their velocities and directions, evidently play no part in producing the wind-bent crowns of this eastern region; furthermore, if winds of easterly direction were of considerably greater velocities in winter than they are here in the eastern gorge they would presumably fail to counteract the influence of the diurnal summer winds. Although west wind here is also the prevailing wind for the year, wind-trained crowns are due to certain peculiar west wind conditions that obtain for perhaps less than half of each day throughout a period of much less than half of each year; it is to be emphasized that this summer period of wind is effective because it coincides essentially with the growing season for the trees.

For any wind velocity, the bending pressure exerted on the branches and twigs of a tree is of course proportional to the extent of the effective surface presented to the air stream by those parts. The extent of surface presented to wind by such evergreen trees as Douglas fir and ponderosa pine may not

[3] According to climatological terminology annual *prevailing wind* refers to the wind of that direction which is maintained for a greater portion of the year than any other; it has no reference to wind velocity or to accompanying peculiar environmental conditions.

fluctuate greatly throughout the year, but deciduous trees, such as Garry oak and Oregon maple, for example, present much greater resistance to wind in summer than in winter; consequently a persistent wind of velocity adequate to maintain the leafy twigs and branches of a tree in wind-bent positions or to break them in a summer period may be quite inadequate to produce permanent deformation when such a tree is without leaves. Also, the earlier portion of the leafy season of the year for deciduous trees coincides with their annual period of most rapid enlargement, when twigs and branches are most readily bent by wind pressure and when they are most likely to remain deformed after the wind that bent them has abated.

While some effects of wind-training may be occasionally observed in most localities where trees grow (Jefferson, 1904), such perfect examples of one-sided crowns as are found in the eastern part of the Columbia Gorge can develop only under very peculiar environmental conditions, in places where neither salt spray nor abrasive materials occur in the air and where wind direction and wind velocity act together in very special ways at recurring periods when the trees concerned are in a physiological state that facilitates wind-pressure deformation and its subsequent fixation by tissue growth and the hardening processes of tissue maturation. The baffling intricacy of the influences that take part in the formation of these remarkable tree crowns is seen to involve climatological, aerological, mechanical, anatomical, and physiological conditions. The ecological problems thus suggested are rendered even more complex and difficult when it is borne in mind that the tendency of a bent branch to straighten and to resist further action of one-sided external pressure not only operates in accordance with the ordinary principles of mechanics but also is generally enhanced through special growth activities that are stimulated by the modified tissue tensions that arise from bending. Much experimental study of pressure effects on trees, as well as much observational study of the natural development of one-sided crowns, will be required before the phenomena here considered superficially may be satisfactorily understood.

SUMMARY

Some of the main physical features of the Columbia Gorge are discussed, including geology, topography, soils, flood history, and tributary drainage systems. Notable vegetational features are described, with special reference to habitat conditions as these differ from west to east and from north to south. The gorge appears to have acted as an east-west corridor for and as a north-south barrier to plant migration.

A number of observations concerning flood tolerance of firs and pines are presented, from which it is concluded that Douglas fir is very intolerant, and that ponderosa pine is considerably more tolerant.

The peculiar and conspicuous one-sided tree crowns of the western and eastern regions of the gorge, especially those of Douglas fir, are described

in detail, with photographic illustrations, and the weather conditions to which these two very different types of crown asymmetry are apparently due are described and discussed.

In the western part, the firs are prevailingly and drastically pruned through mechanical breakage due to the action of occasional easterly winter gales that are accompanied by heavy deposition of ice. These crowns characteristically extend only in a westerly direction from the trunks. The firs of the western part are also characteristically subject to parch blight in many instances, a form of injury in which the foliage and branchlets on many unbroken branches are winter-killed. The killed needles gradually become brown as spring comes on but they generally remain in position for several months, giving rise to discolored patches that are conspicuous in spring and early summer.

In the eastern part, the firs show little or no signs of storm breakage or parch blight, but they are characteristically wind-trained, through the action of persistent strong westerly winds of summer; their crowns generally extend only in an easterly direction from their trunks, branches arising on the west being bent around the trunks so as to extend toward the east.

In the middle region of the gorge, in the vicinity of the Cascade Rapids, both forms of fir crown may be seen, and some crowns exhibit the combined effects of both storm-pruning in winter and wind-training in summer.

The western, storm-pruned type of tree asymmetry resulting chiefly from glaze injury has apparently not been described for any other part of the world; but the eastern, wind-trained type is not uncommon in localities where strong winds of persistent direction and velocity occur in the growing season.

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MAPS CITED

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2. United States Geol. Surv. Topographic Sheets:—(a) Troutdale Quadrangle, Oregon-Washington; south of the river 1918, north of the river 1934. (b) Mount Hood and Vicinity, Oregon-Washington. 1913. (Reprinted 1926) (c) Hood River Quadrangle, Washington-Oregon. 1929. (d) The Dalles Quadrangle, Washington-Oregon; south of the river 1934, north of the river incomplete, but photostatic sheet showing water courses and some contours is available.

3. United States War Department, Corps of Army Engineers. Columbia River Chart:—Vancouver to The Dalles, Oregon and Washington, surveyed October 1917 to March 1918. Sheets 2, 3, 4, and 5.